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Founded by J. A. Nieuwland, C.S.C.

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A Guide to the Flowering Plants and Ferns of the Western National Parks

Virginia Long Bailey and Harold Edwards Bailey

Wayne University, Detroit, Michigan

Introduction

The purpose of this work is to bring together in one treatment the plant species known to occur within the boundaries of the sixteen national parks of the western United States and Alaska (fig. 1). Many visitors to the national parks are interested in observing the similarities and differences in vegetation as they pass from one area to another. In this region, where there are striking differences in topographic features as well as considerable range in elevation and in latitude, it is possible within comparatively short distances to observe a great many types of vegetation from sea level to Arctic-Alpine or from Lower Sonoran desert to humid forest with a great many variations and modifications in between. It is hoped that this guide will not only help in identification of the plants, but also provide a comprehensive means of comparison of the species found in the different regions and suggest some of those to be expected in other areas.

The check lists of localities, i.e. park areas in which each species occurs, is a compilation of all data available from herbarium specimens and from various publications. In addition to observations and plant collections made in the western national parks by the authors over a period of years from 1935 to 1950, the following herbarium collections have been examined:

1. Vegetation type map collections made during a vegetation survey of the western national parks (1935 to 1938) under the direction of the Division of Forestry of the U. S. National Park Service. Duplicates of the specimens are in the University of California herbarium at Berkeley.
2. California Forest Experiment Station collections made in California park areas during the state vegetation survey begun in 1934. These were examined in the California Forest Experiment Station herbarium at Berkeley.
3. Collections made in the Sierra Nevada parks of California, particularly by John Thomas Howell (California Academy of Sciences herbarium in San Francisco), working out from the Sierra Club base camps during the summers of 1940, 1942, 1944, 1948, 1949, and 1952 (Peter H. Raven). The "Base Camp Botany" lists distributed as Sierra Club contributions, mostly in mimeographed form, have proved very valuable and from these, several hitherto unreported species have been added to the park lists.
4. Herbarium collections maintained in each of the parks as a part of the naturalist service and serving as a basis for small park floras available for several of the western parks. Those parks which do not as yet have published floras mostly have at least mimeographed lists of the plants known to occur in the respective areas.

FIG. 1.—Map showing location of western National Parks.

5. Several collections from the western United States in the University of Michigan herbarium at Ann Arbor, including those of Dr. Elzada Clover along the Colorado River in Grand Canyon National Park, have also added to the species known to occur in the western parks.

In addition to the publications of floras and check lists referred to above, various state and regional floras have been consulted and will prove very useful to users of this work for checking descriptions of the species. For a list of some of these, the reader is referred to bibliographies in two previous publica-

tions on the trees and shrubs of the western national parks.[1,2] These also include descriptions of the trees and shrubs respectively. Also, the following publications on the flora of Alaska should be mentioned: 1) *Pocket Guide to Alaska Trees*, by R. F. Taylor and E. L. Little, Jr.;[3] 2) *Flora of Alaska and Adjacent Parts of Canada*, parts I-IX, by J. P. Anderson;[4] 3) *Flora of Alaska and Yukon*, parts 1-10, by Eric Hulten.[5]

The scientific names used are those accepted as valid according to the International Rules of Botanical Nomenclature by recognized authorities for various groups, or those used in standard botanical floras. Names for the trees are according to those accepted by the United States Forest Service Tree and Range Plant Name Committee and used in the 1953 Check List of Trees of the United States.[6] Common names have been given in parentheses, but the scientific or Latin names are essential to an understanding of the true identity of a species. Synonyms are given generally only for those species listed under different names in the park floras or in the plant lists compiled by the park service.

The text is composed principally of keys for the identification of families, genera, and species. The metric system of measurement is used for designation of the size of plants and plant parts. For those not accustomed to using this system, the following may be helpful: one meter (1 m.) equals approximately 39 inches; 2.5 centimeters (2.5 cm), about 1 inch; one millimeter (1 mm), 0.1 cm. The average size range is generally given, but in some instances where there are notable exceptions to this range, the less usually found maximum or minimum is indicated by a figure in parentheses.

In order to save space and thus reduce the size of the volume so that it will not be too large for practical use, descriptions of species have been omitted. In the specific and generic keys, similarities and general relationships of groups are shown as much as possible by position in the keys, but in the distribution paragraph for each genus, the species are arranged alphabetically for the convenience of the user. Occurrence is indicated by symbols representing the various park areas. The sequence is in order of the location of the regions from west to east, and of the parks from north to south in each of the three regions, as shown in table 1.

Geographical Regions and Plant Distribution

The wide geographic range occupied by the sixteen national parks of the United States from the continental divide west, and the consequent differences

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[1] Bailey, H. E. and V. L., Forests and Trees of the Western National Parks. United States Department of the Interior, Conservation Bulletin No. 6, 1941.

[2] Bailey, V. L. and H. E., Woody Plants of the Western National Parks. American Midland Naturalist, Monograph No. 4, 1949.

[3] Agriculture Handbook no. 5. U. S. Dept. Agr., Forest Service. 1950.

[4] Iowa State College J. Sci. 18:137-175, 381-445. 1943, 1944; 19:133-205. 1945; 20:213-257, 297-347. 1946; 21:363-423. 1947; 23:137-187. 1949; 24:219-271. 1950; 26:387-453. 1952.

[5] Lunds Univ. Arsskr., N. F., Avd. 2, 37:1-127. 1941; 38:129-412. 1942; 39:413-567. 1943; 40:569-795. 1944; 41:797-978. 1945; 42:979-1066. 1946; 43:1067-1200. 1947; 44:1203-1341. 1948; 45:1345-1481. 1949; 46:1485-1902. 1950.

[6] Agriculture Handbook no. 41. U. S. Dept. Agr., Forest Service. 1953.

TABLE 1.

PACIFIC SLOPE REGION		ROCKY MOUNTAIN REGION	
Alaska Range		*Northern Province*	
Mount KcKinley National Park	**MK**	Glacier National Park	**G**
Pacific Northwest		*Middle Province*	
Olympic National Park	**O**	Yellowstone National Park	**Yl**
Mount Rainier National Park	**MR**	Grand Teton National Park	**GT**
Southern Cascades		*Southern Province*	
Crater Lake National Park	**C**	Rocky Mountain National Park	**RM**
Lassen Volcanic National Park	**L**	SOUTHWEST REGION (Colorado Plateaus)	
Sierra Nevada		Mesa Verde National Park	**MV**
Yosemite National Park	**Yo**	Bryce Canyon National Park	**B**
Kings Canyon National Park	**K**	Zion National Park	**Z**
Sequoia National Park	**S**	Grand Canyon National Park	**GC**

in climatic and habitat conditions, offer unusual opportunities for a comparison of a wide variety of vegetation types as well as for observations as to some of the determining factors in plant distribution. Geographically these areas may be grouped into three rather well-defined regions (table 1 and fig. 1): 1) Pacific Slope region, including the series of far-western mountains ranging from Alaska to Mexico and draining west to the Pacific Ocean; 2) Rocky Mountain region, including the ranges of mountains along the continental divide from the British Columbia and Alberta boundary south through western Montana and Wyoming to Colorado; 3) Southwest region, a high plateau region cut by the Colorado River and its tributaries.

PACIFIC SLOPE REGION

Eight of the western national parks are located in the far western mountain ranges of the Pacific slope. Farthest north, only a few degrees south of the Arctic Circle, is Mount McKinley National Park located in the Alaska Range of Central Alaska. Mount McKinley itself, rising to an altitude of 20,300 feet above sea level, is the highest peak on the North American continent. The perpetually ice-covered mountain rises abruptly from a relatively low plateau which is only about 2,500 to 3,000 feet in elevation. Since the limit of trees in that northern latitude is at about 3,000 feet, much of the park area is above timberline. Open slopes are covered with a spongy tundra-like type of formation consisting of sphagnum moss and a low heath type of plants. Members of the family Ericaceae predominate. Dwarf alpine willows (*Salix anglorum*, *S. reticulata*, and *S. rotundifolia* are also common. Low wet *pot holes* or depressions are occupied by dense mats of sedge and several types of water plants.

The forests of the lowest elevations in the park, about 2,500 feet and below, are predominantly white spruce (*Picea glauca*). Black spruce (*P. mariana*) and tamarack or eastern larch (*Larix laricina*) are much less common in the lower boggy areas. A transition type between forest and tundra is characterized by thickets of dwarf birch (*Betula glandulosa* and its many forms). Black cottonwood, aspen, and tall shrubby willows are found along the lower streams.

Moving southward to the United States proper, the first parks encountered are Mount Rainier and Olympic National parks in northwestern Washington. These two areas may be considered as representative of the Pacific Northwest,

characterized by an exceedingly dense and luxuriant forest type of vegetation cover. Elevations range from sea level along the coastal strip of Olympic National Park to 14,408 feet at the top of Mount Rainier. The geographical location, west of the Cascade crest and relatively close to the ocean, is responsible for the generally mild climate with annual precipitation ranging from 60 to 100 inches at Mount Rainier and to 144 inches on the west side of the Olympic Peninsula.

Lowland forests, up to about 3,000 feet, are composed primarily of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Although undercover plants are not abundant under the dense tree canopy, several shrubby species are frequently found. Among those of frequent occurrence are highbush whortleberry species (*Vaccinium parvifolium* and *V. ovalifolium*) and salal (*Gaultheria shallon*). Broadleaf trees such as red alder (*Alnus rubra*), black cottonwood (*Populus trichocarpa*), and bigleaf maple (*Acer macrophyllum*) occur along streams along with species of willow (*Salix*) and occasionally red-osier dogwood (*Cornus stolonifera*).

Forest trees of this lower zone are gradually replaced above by more open stands of mountain hemlock (*Tsuga mertensiana,*), Alaska cedar (*Chamaecyparis nootkatensis*), and species of fir (*Abies*). In the upper part of this zone and up to timberline subalpine fir (*A. lasiocarpa*) is the dominant fir species. Some of the undercover shrubs found in the middle forest are Pacific red elder (*Sambucus callicarpa*), Rocky Mountain maple (*Acer glabrum*), rusty menziesia (*Menziesia ferruginea*), western thimbleberry (*Rubus parviflorus*), big whortleberry (*Vaccinium membranaceum*), vine maple (*Acer circinatum*), and species of gooseberry and currant (*Ribes*).

Alpine fir and mountain hemlock form open park-like stands or scattered clumps in the subalpine grassland areas above 4,500 feet. Low shrubby plants of the heath family (Ericaceae) are characteristic of the ground cover, along with grasses, sedges, dwarf willows, and the many colorful flowering herbaceous species. Many of these extend into the arctic-alpine zone above the limit of trees, sometimes as far up as 10,000 feet in sheltered nooks on the slopes of Mount Rainier.

Continuing towards the south, we come to the southern end of the Cascade Mountains in southern Oregon and northern California in which are located Crater Lake and Lassen Volcanic National Parks. Evidences of volcanic activity which was responsible for the major features of these two parks may be seen in large areas covered with a soil mantle of pumice, tuff or other debris of volcanic origin. Located in the inner range of mountains and separated from the ocean by intervening ranges and valleys, these areas have a drier climate with greater extremes of temperature than in the parks of the Pacific northwest.

The lower forests, up to about 5,500 feet at Crater Lake, are composed of Douglas fir, ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense cedar (*Libocedrus decurrens*), and sugar pine (*Pinus lambertiana*). Since most of the area within the boundaries of Lassen Volcanic National Park is above the range of these species, they are not important in the flora there. A higher elevation form of yellow pine, *Pinus jeffreyi,* occurs along with white fir in place of the ponderosa pine. In both areas western white pine

(*Pinus monticola*) and lodgepole pine (*Pinus contorta*) gradually become dominant above 5,500 feet, along with red fir (*Abies magnifica* or its var. *shastensis*) and mountain hemlock. The latter becomes the dominant species at the higher elevations up to timberline. Whitebark pine (*Pinus albicaulis*) follows the ridges nearly to 10,000 feet on Mount Lassen. White fir, incense cedar, and sugar pine, which are characteristic species further south in the Sierra Nevada, reach their northern limits of distribution at Crater Lake National Park. Shrub species frequent in forest openings in both park areas include pinemat manzanita (*Arctostaphylos nevadensis*), subalpine spiraea (*Spiraea densiflora*), and species of gooseberry and currant. Shrubby alders (*Alnus* sp.) and willows (*Salix* sp.) are common along streams.

To the south the Cascade Range divides into the Coast Range and the Sierra Nevada which forms an unbroken range of mountains separating the Great Basin area of Nevada from the Great Valleys of middle California. Along the western slope of this range and all within 100 miles are located three national parks, Yosemite National Park and the jointly-administered Kings Canyon and Sequoia National parks. All of these areas are characterized by broad deep glacial valleys and smooth granite dome formations in the high country. Elevations range from about 1,500 feet, in the foothills along the western boundaries, to the Sierra crest, which forms the eastern boundary of each of the three parks. Along this crest the highest elevation, at the top of Mount Whitney in Sequoia National Park (14,501 feet), is also the highest point in the United States proper.

In the dry lower foothill areas the vegetation is of an open grassland type with scattered oak trees (*Quercus* sp.), and various shrubby species such as buckbrush ceanothus (*Ceanothus cuneatus*), manzanita (*Arctostaphylos* sp.), birchleaf mountain mahogany (*Cercocarpus betuloides*), yerba santa (*Eriodictyon californicum*), greasewood chamise (*Adenostoma fasciculatum*), and shrubby oaks.

Above the foothill area is a quite uniform forest belt composed mainly of ponderosa pine, sugar pine, white fir, and incense cedar up to about 6,500 or 7,000 feet. Of particular interest in this zone are the many groves of bigtree (*Sequoia gigantea*) in which are found the famous giant trees such as the Wawona tree in Yosemite National Park, the General Sherman tree at Giant Forest in Sequoia National Park, and the General Grant tree in the General Grant Grove section of Kings Canyon National Park. This latter tree has been dedicated as the Nation's Christmas tree.

In the upper part of this forest belt, the trees are gradually replaced by Jeffrey pine (*Pinus jeffreyi*) and red fir (*Abies magnifica* or its var. *shastensis*) which remain dominant up to about 9,000 feet. Species of manzanita (*Arctostaphylos*) and *Ceanothus* are frequent associates, along with California chinquapin (*Castanopsis sempervirens*) and western thimbleberry (*Rubus parviflorus*). At higher elevations lodgepole pine covers considerable area, along with mountain hemlock in Yosemite and Kings Canyon National parks, or with foxtail pine (*Pinus balfouriana*) in Sequoia and Kings Canyon National parks. Whitebark pine and Sierra juniper (*Juniperus occidentalis*) occur on ridges and nearly barren granite slopes up to timberline. Above timberline, at around 11,000 to 12,000 feet, many showy alpine flowering species occur in sheltered ravines, at the base of rock outcrops, or in other favorable locations.

ROCKY MOUNTAIN REGION

The Rocky Mountain region, as interpreted here, covers an extensive area of mountain ranges from the international boundary in northwestern Montana south to middle Colorado. In spite of the extensive area covered, and the variety of climatic and topographic conditions, the forest cover is, in general remarkably uniform. Lodgepole pine (*Pinus contorta*) is the dominant species over a considerable part of the areas included in the four national parks of this region, while at higher elevations and up to timberline Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*) become more important in the forest. These form picturesque tree islands in the open park-like subalpine meadows or grasslands. Douglas fir (*Pseudotsuga menziesii* var. *glauca*) is widespread in the more protected moist areas and limber pine (*Pinus flexilis*) is frequent in many types of habitats, especially on open exposed slopes and ridges at the higher elevations. The prevalence of lodgepole pine as well as the widespread occurrence of quaking aspen (*Populus tremuloides*) indicates that fires have been common throughout the region in times past.

Shrub species commonly associated with these forests include mountain ash (*Sorbus scopulina*), black chokecherry (*Prunus virginiana* var. *melanocarpa*), western red raspberry (*Rubus idaeus* var. *aculeatissimus*), black twinberry (*Lonicera involucrata*), Rocky Mountain maple (*Acer glabrum*), mountain common juniper (*Juniperus communis* var. *saxatilis*), creeping hollygrape (*Berberis repens*), wild rose (*Rosa* sp.), willows (*Salix* sp.), and alders (*Alnus* sp.). Shrubby cinquefoil (*Potentilla fruticosa*) and bearberry (*Arctostaphylos uva-ursi*) are frequent in open rocky areas. In the subalpine areas and above are such species as red mountain heath (*Phyllodoce empetriformis*), alpine laurel (*Kalmia polifolia* var. *microphylla*), white mountain dryad (*Dryas octopetala*), alpine willows, and many showy-flowered herbaceous species as well as numerous grasses and sedges.

Influences of climatic, topographic and geologic factors, as well as differences in latitude, have given rise to various local types of floras in different parts of the region. In Glacier National Park, in northwestern Montana, influences of the moist climate of the Pacific northwest are evident in the type of forest in certain areas on the west side of the continental divide. In valleys which have escaped the ravages of fire for a number of years, notably the McDonald Valley, there prevails a dense cedar-hemlock forest composed primarily of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and species found also in the lowland forests of the Pacific northwest. Western white pine (*Pinus monticola*) and lowland white fir (*Abies grandis*) are frequent associates, as well as Douglas fir, Engelmann spruce, and in some places western larch (*Larix occidentalis*).

A number of species occurring commonly in the northern and middle provinces of western Montana and Wyoming are not found in Rocky Mountain National Park in Colorado. Among these are whitebark pine (*Pinus albicaulis*), western thimbleberry (*Rubus parviflorus*), rusty menziesia (*Menziesia ferruginea*), Utah honeysuckle (*Lonicera utahensis*), bigleaf whortleberry (*Vaccinium membranaceum*), and at the higher elevations subalpine spiraea, which ranges south into the Sierra Nevada parks of California but does not extend into the southern Rocky Mountains.

The vegetation cover in Rocky Mountain National Park, in many respects, shows relationships with the dry desert-plateau areas of the southwest region. Some of the species include bush rockspiraea (*Holodiscus discolor* var. *dumosa*), wax currant (*Ribes cereum*), bitterbrush (*Purshia tridentata*), boulder raspberry (*Rubus deliciosus*), and Parry Rabbitbrush (*Chrysothamnus parryi*).

Species of currant and gooseberry (*Ribes* sp.) have been abundant in the parks of the Pacific slope and of the Rocky Mountains, but the Forest Service program of *Ribes* eradication in order to save the white pines from ravages of blister rust has resulted in the near elimination of some of the currant and gooseberry species from these areas.

SOUTHWEST REGION

The region here designated as Southwest includes the high Colorado plateau areas of southern Utah, southwestern Colorado, Northwestern New Mexico, and northern Arizona. It is mainly a tableland region over 5,000 feet in elevation cut into irregular plateaus and mesas by the Colorado River and its tributaries. Noted features are the high cliffs and spectacular formations carved out by weathering in the colorful sandstones and limestones making up the rock strata. These sedimentary rocks are soft and easily eroded, and the plant growth in that dry desert climate is not dense enough to bind the soil and provide adequate protection against the torrential rains and strong winds which buffet the region during certain seasons.

Mesa tops or plateaus are mainly forested. The lower plateaus, up to about 7,500 or 8,000 feet, are covered with a piñon-juniper forest type in which the 2-needle piñon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) or Rocky Mountain juniper (*Juniperus scopulorum*) are the dominant tree species. Shrubby associates include species of serviceberry (*Amelanchier* sp.), mountain mahogany (*Cercocarpus montanus*), cliffrose (*Cowania stansburiana*), fendlera (*Fendlera rupicola*), antelope bitterbrush (*Purshia tridentata*), lemonade or skunkbush sumac (*Rhus trilobata*), Gambel oak (*Quercus gambelii*), and occasionally Spanish bayonet (*Yucca baccata*) and species of cacti.

At elevations above 7,500 feet ponderosa pine (*Pinus ponderosa*) becomes an important forest tree, forming the dominant cover over most of the plateau areas at Bryce Canyon and Zion National parks and on the north rim of the Grand Canyon. In pure dense stands there is scarcely any undercover growth, but where the trees are more scattered several shrub species may be found, such as manzanita (*Arctostaphylos patula*), blueberry elder (*Sambucus coerulea*), mountain mahogany, antelope bitterbrush, Rocky Mountain white oak (*Quercus utahensis*), serviceberry species, snowberry (*Symphoricarpos rotundifolius*), big sagebrush (*Artemisia tridentata*), and wax currant (*Ribes cereum*).

At the higher elevations, as at the south end of the plateau at Bryce Canyon National Park and on the north rim of the Grand Canyon, white fir (*Abies concolor*) and Douglas fir (*Pseudotsuga menziesii* var. *glauca*) occur along with the ponderosa pine and gradually replace it. Douglas fir is found also at lower elevations in cooler moist or shaded canyons, such as in Spruce Canyon below park headquarters at Mesa Verde National Park, and in sheltered pockets below the south rim of the Grand Canyon.

The vegetation of the talus slopes and canyon bottoms shows considerable diversity when considered for the whole region, but general similarities in appearance as well as in species composition may be noted. The perpendicular cliff walls and very steep slopes are for the most part barren. The upper talus slopes support sparse stands of piñon-juniper, oaks, and many shrubby species characteristic of the piñon-juniper forests of the plateaus. Singleleaf piñon (*Pinus monophylla*) is sometimes found in the association. A few species of desert shrubs characteristic of the lower talus slopes and dry valley flats are wolfberry (*Lycium pallidum*), snakeweed (*Gutierrezia sarothrae*), species of rabbitbrush (*Chrysothamnus* sp.), blackbrush (*Coleogyne ramosissima*), four-wing saltbush (*Atriplex canescens*), and species of horsebrush (*Tetradymia* sp.).

Permanent streams along the valley floors are lined with broadleaf species such as cottonwood (*Populus fremontii*), willows (*Salix gooddingii, S. laevigata,* and *S. exigua*), boxelder (*Acer negundo* var. *interius*), and desert ash (*Fraxinus velutina* var.). Bigtooth maple (*Acer grandidentatum*) is also common around springs or on slopes, along with desert ash and box elder.

Pteridophyta. Ferns and Fern-like Plants.

Plants reproducing by spores, never bearing flowers or seeds.

KEY TO THE FAMILIES

Leafblades flattened and distinctly leaf-like; spores borne in minute sporangia, microscopic in size, borne on the under surfaces of the leafblades, or the spores enclosed in coarser pod-like sporangia formed by modifications of the fertile leafblades.

- Plants terrestrial; leaves (fronds) mostly large and conspicuous, fern-like, the petioles (leafstalks) more or less erect from underground stems; spores of one kind.
  - Leafstalks arising singly or few together, bearing a single sterile leafblade below and a fertile upper portion which is variously divided into globular somewhat pod-like sporangia; leaves not coiled in the bud. ....(Adder's Tongue Family) OPHIOGLOSSACEAE, p. 10
  - Leafstalks arising singly or densely clustered; sporangia borne in small clusters (sori) or along the veins on the backs of the leafblades, or in a more or less continuous band along the margin; leaves coiled in the bud, the fertile and sterile rarely of different types. ....(Fern Family) POLYPODIACEAE, p. 11
- Plants aquatic, free-floating or rooting in the mud; leafblades small, mostly less than 1 cm long; spores of two sizes.
  - Leaves 4 to 8 cm long, from slender creeping stems rooting in the mud; petioles to 6 cm long; leafblades usually divided into 4 segments about 4 to 10 mm long, resembling 4-leaf clover leaves; pod-like spore-bearing structures borne on erect stems only about 0.5 to 1.5 cm high and united at base with base of petioles. ....(Pepperwort Family) MARSILIACEAE, p. 20
  - Leaves about 1 mm long, not stalked or scarcely, borne close together along the floating stems in two ranks (apparently), the stems without roots or with simple rootlets; pod-like spore-bearing structures borne in the axils of some of the leaves. ....(Floating Moss Family) SALVINIACEAE, p. 20

Leafblades scale-like, awl-shaped, needle-like, or long-tubular and appearing grass-like; sporangia (spore-cases) borne in terminal cone-like structures or in the axils of the leaves.

Stems conspicuously jointed, the joints easily separated; leaves reduced to membranous scales joined in a sheath around each joint; sporangia borne in terminal cone-like structures ....(Horsetail Family) EQUISETACEAE, p. 20

Stems not conspicuously jointed, densely covered by the leaves, or the leaves long-tubular, grass-like and clustered at the base.

Leaves scale-like, awl-shaped, or needle-like, closely covering the stems; plants terrestrial, often in moist woods; sporangia borne in the axils of the upper leaves or in modified cone-like structures at the ends of erect branches.

Spores all of one size, mostly borne in cone-like structures (except *Lycopodium selago*) ....(Clubmoss Family) LYCOPODIACEAE, p. 21

Spores of two sizes, the smaller borne in sporangia in the upper leaf axils, the larger commonly in groups of 4 in lobed sporangia in the leaf axils immediately below, the spore-bearing leaves not forming distinct cone-like structures ......(Selaginella Family) SELAGINELLACEAE, p. 22

Leaves long-tubular, grass-like or quill-like, clustered; sporangia borne in the axils of the broadened leaf bases and usually more or less covered by membranous margins (vellum); spores of two sizes, the larger borne in sporangia in the outer leaf-axils; plants aquatic or rooting in the mud ....(Quilwort Family) ISOETACEAE, p. 23

OPHIOGLOSSACEAE—Adder's Tongue Family

KEY TO GENERA

Sterile leafblade (in ours) mostly lobed or divided into segments (rarely only shallowly lobed), the vein branches ending in free tips; pod-like sporangia borne in simple spikes or more commonly in branched clusters, often close together but not actually cohering......................(Grape Fern) BOTRYCHIUM, p. 10

Leafblade (in ours) simple, not at all toothed nor lobed, the veins conspicuously branched and forming an interlocking network; pod-like sporangia borne in a simple spike, the sporangia closely adhering in two rows.. (Adder's Tongue) OPHIOGLOSSUM, p. 11

BOTRYCHIUM (Grape Fern)

KEY TO THE SPECIES

Sterile leafblade simple, lobed, or once-divided, the final segments fan-shaped, with broad rounded tips, mostly wider than long, often overlapping.

Sterile leafblade stalked, usually borne below middle of stem or only slightly above, 1 to 5 cm long, 0.5 to 2.5 cm wide; plants rather weak and slender, 3 to 15 (25) cm high; found mostly in Sierra Nevada.

Sterile leafblade once-parted or divided with few to several segments.. *B. simplex*

Sterile leafblade divided into 3 parts, the lower divisions long-stalked and usually lobed .... var. *compositum*

Sterile leafblade not stalked, the blade apparently arising directly from the stem; plants mostly stout and fleshy, 4 to 30 cm high.

Sterile leafblade oblong to ovate or reverse-ovate, 1 to 12 cm long, 1 to 5 cm broad, once-divided into fan-shaped or nearly kidney-shaped segments; widespread in the western parks. *B. lunaria*

Sterile leafblade triangular, 2 to 4 cm long, 1.5 to 4 cm broad, divided into 3 main segments, these again divided into broad-tipped or variously lobed segments; found in pumice gravel at Crater Lake .... *B. pumicola*

Sterile leafblade once- to several-times parted or divided, the final segments longer than wide, mostly scarcely stalked (usually long-stalked in *B. multifidum*).

Sterile leafblade oblong to ovate or triangular, once- or twice-divided, the final segments oblong to ovate or narrowly fan-shaped; bud for next year's stalk glabrous; plants 3 to 25 cm high; found in Northwest and Rocky Mountains, not common.

(*Following species not well differentiated.*)

Sterile leafblade narrowly-triangular.

Sterile leafblade with acute segments .... *B. lanceolatum*

Sterile leafblade with obtuse or rounded segments.

Found in northern and central Colorado.................................
.... *B. matricariaefolium* subsp. *hesperium*

Found in Alaska and northern Rocky Mountains ....
.... *B. boreale* and var.

Sterile leafblade oblong; found at Mount Rainier.................... *B. pinnatum*

Sterile leafblade broadly triangular, mostly 3-times divided, at least below; bud for next year's stalk hairy; plants 10 to 75 cm high.

Sterile leafblade usually long-stalked from lower part of stem; bud hidden by sheathing base of stem; widespread on Pacific slope and middle Rocky Mountains .... *B. multifidum* and subsp.

Sterile leafblade arising from upper part of stem and not stalked; northern species rarely found in the western parks.................................
.... *B. virginianum* var. *europaeum*

OCCURRENCE.—*Botrychium boreale*: (MK) (reported); var. *obtusilobum*: (G); *lanceolatum*: (O, MR, Yl); *lunaria* (including vars. *minganense* and *onondagense*): (MK, O, S, G, Yl); *matricariaefolium* subsp. *hesperium*: (RM); *multifidum* (including subsp. *californicum*, *coulteri*, and *silaifolium*): (O, MR, Yo, K, S, G, Yl, GT); *pinnatum*: (MR); *pumicola*: (C); *simplex* and var. *compositum*: (Yo, K, S, reported from Yl, RM); *virginianum* var. *europaeum*: (G).

OPHIOGLOSSUM (Adder's Tongue)

OCCURRENCE.—*Ophioglossum vulgatum*: (O).

POLYPODIACEAE—Fern Family

KEY TO GENERA

Leafblades once-divided (1-pinnate), or if 2-pinnate, the plants coarse and the leaf segments with awned teeth or finely spine-toothed.

Coarse plants with sterile and fertile fronds (leaves) distinctly different; sterile fronds (15) 30 to 100 cm long, the blades narrowly lance-shaped from a narrowed base, the leaflets narrowly oblong, becoming gradually shorter towards both ends of fronds; fertile fronds 40 to 150 cm long, arising from center of sterile cluster, the blades similar, but with narrowly linear segments more distantly spaced on axis; sporangia covering the lower surface of segments; Pacific northwest, in moist forests. (*Struthiopteris spicant*)..
.... (Deer Fern) *Blechnum spicant*, p. 14

Coarse or delicate plants with sterile and fertile fronds not distinctly different; sporangia borne in definite groups (sori) on the backs of the leaf segments.

Sori roundish or oval.

Leaf segments not toothed or very shallowly so; sori without membranous covering (indusium); fronds (10) 20 to 40 (70) cm long, generally arising singly from slender creeping rhizomes ....(Polypody) POLYPODIUM, p. 14

Leaf segments toothed, with generally long-pointed or awned teeth; sori covered by peltate (umbrella-like) indusium attached at center of sorus; fronds to 40, 60, or 100 (180) cm long, clustered ....
.... (Shield Fern) POLYSTICHUM, p. 14

Sori oblong to linear, with indusium attached on one side, along the length of the sorus.

Fronds large, 90 to 200 or more cm long, the blades narrowly oblong to oblong-ovate, twice-divided (2-pinnate), lance-shaped to linear-triangular segments, these finely spine-toothed; sori borne end to end in 2 parallel rows on either side of midrib; lower elevations in California parks ....(Giant Chain Fern) *Woodwardia radicans*, p. 15

Fronds smaller, generally less than 30 cm long, the blades narrowly oblong to linear, 1-pinnate (in ours), the segments narrowly linear to oval or broadly oblong; sori borne more or less parallel to branch veins of leaf segments, those on opposite sides of veins sometimes running together as a large irregular sorus; northwest and Rocky Mountain parks......(Spleenwort) ASPLENIUM, p. 15

Leafblades mostly 2- to 3-times divided, or if only 1-pinnate, the sporangia borne along margins of leaf segments and usually at least partially covered by inrolled leaf margin; leaf segments often toothed or lobed, but not spine-toothed or awn-toothed; plants coarse or fragile.

Sporangia borne in continuous or interrupted band along margins of leaf segments, usually at least partially covered by inrolled margin of leaf.

Fronds rarely more than 30 (40) cm long, mostly clustered.

Fronds few or loosely clustered; fragile ferns with slender, usually dark shiny leafstalks; blades with segments broadly wedge-shaped to roundish or oblong-fan-shaped, with main veins spreading from point of attachment; commonly found in moist shaded locations.............................. (Maidenhair) ADIANTUM, p. 15

Plants strongly tufted; fronds with segments often strongly inrolled and appearing linear or narrowly lance-shaped to nearly globose and beadlike; favoring rocky open slopes and rock crevices.

Leafblades generally glabrous, not scaly or hairy, sometimes with a whitish powdery bloom; sporangia in a continuous marginal band, usually covered by inrolled margin of segments.

Sterile and fertile fronds distinctly different; sterile fronds relatively short-stalked, the blades with irregularly divided segments, flat; fertile fronds arising in center of sterile cluster, the segments of blades fewer, with strongly inrolled margins covering marginal band of sporangia .... (Rock Brake) CRYPTOGRAMMA, p. 15

Sterile and fertile fronds not distinctly different, all similar to fertile fronds of *Cryptogramma*..........(Cliff Brake) PELLAEA, p. 16

Leafblades (in ours) mostly densely woolly or scaly, at least below (except *Cheilanthes californica*); sporangial band at first interrupted, often becoming confluent at maturity.

Leafblades 2- to several-times divided, the final divisions often very small and bead-like, 1 to 2 mm long, densely hairy or scaly or both, at least on veins below (glabrous in *Cheilanthes californica*), the margins strongly inrolled................ (Lace Fern, Lip Fern) CHEILANTHES, p. 17

Leafblades once-divided, the segments 0.5 to 1 cm long, oval or roundish to egg-shaped, the margins lobed and not strongly inrolled, densely covered beneath by overlapping, hairy-fringed scales; southwest, not common .... (Cloak Fern) *Notholaena sinuata*, p. 17

Fronds 30 to 200 cm long, arising singly from widely spreading underground stems (rhizomes); leafstalks stout, erect, 15 to 100 cm long; blades about as long, spreading at more or less right angles to the stalks, divided into 3 short-stalked parts, these again twice divided into deeply lobed or divided segments; widespread in western parks in dry open woods and clearings, especially in burned areas ....(Western Bracken) ***Pteridium aquilinum* var. *pubescens***, p. 17

Sporangia borne in definite sori or rarely following the vein lines beneath; sori naked or with thin indusium.

Fronds with blades narrowly triangular or ovate to oblong, lance-shaped, or linear, (1) 2- to 3 (4)-pinnate, generally erect or spreading in same line with the stalks; leafstalks mostly not longer than blades (longer in *Cystopteris montana*).

Fronds strongly tufted; sori roundish; indusium, if present, broadly attached on one side or spreading from underneath.

Indusium present (sometimes not evident); fronds not usually exceeding 50 cm in length.

Blades of fronds mostly 2- or 3 (4)-pinnate, often resembling *Woodsia* in appearance; sori covered by hood-like indusium broadly attached from one side, in maturity often folded back and not evident......... (Bladder Fern) CYSTOPTERIS, p. 18

Blades of fronds (1) 2-pinnate; sori with toothed or fringed indusium spreading from underneath, sometimes nearly hidden by sporangia. ....(Woodsia) WOODSIA, p. 18

Indusium lacking; fronds 20 to 90 cm long, the blades 2- to 3-pinnate. .... (Alpine Lady Fern) *Athyrium alpestre*, p. 18

Fronds tufted or not; sori curved-oblong or kidney-shaped to roundish-horsheshoe-shaped, the indusium attached at the notch or on the inner curve and often nearly covering sorus.

Fronds usually large, up to 180 cm long, loosely clustered; sori small, usually less than 1 mm long, tending to be short-oblong to crescent-shaped or horseshoe-shaped; widespread and variable species; Pacific slope and Rocky Mountains .... (Lady Fern) *Athyrium filix-femina*, p. 18

Fronds small to large (up to 120 cm long), clustered or not; sori large or small, more uniformly roundish-kidney-shaped, with indusium attached at notch. .... (Wood Fern) DRYOPTERIS, p. 19

Fronds with blades broadly triangular, divided into 3 nearly equal parts, these again divided into deeply lobed or divided segments; leafstalks generally much longer than blades, the blades often tending to spread more or less horizontally from the stalks.

Fronds arising singly, 20 to 60 cm long; blades glabrous and green below, the 3 main divisions stalked; sporangia borne

in distinct roundish sori, without indusium; common in woods, in northwest and Rocky Mountains. (*Dryopteris linnaeana*). .... (Oak Fern) *Dryopteris disjuncta*, p. 19

Fronds clustered, 15 to 40 cm long; blades characteristically yellowish-powdery below, the two lower divisions not stalked; sporangia borne along veinlets below and finally covering the surface; Pacific slope parks, at lower elevations. (Gold Fern) *Pityrogramma triangularis*, p. 19

BLECHNUM (Deer Fern)

OCCURRENCE.—*Blechnum spicant* (*Struthiopteris spicant*): (O, MR).

POLYPODIUM (Polypody)

KEY TO THE SPECIES

Leafblades thick and leathery, triangular-ovate, the midribs scaly at first; sori large, 3 to 4 mm broad; fronds 15 to 70 cm long; humid coastal zone in northwest............ (Coast Polypody) *P. scouleri.*

Leafblades herbaceous, lanceolate or oblong, the midribs not scaly; sori smaller, 1 to 2 mm long; species extending into interior and to higher elevations (*P. vulgare* of auth., not L., and vars.).

Fronds mostly more than 20 cm long, the stalks usually shorter than the blades; leaf segments linear-oblong; Pacific slope parks.

Fronds 20 to 70 cm long, the blades usually lanceolate, with segments pointed; veins mostly translucent; mostly in northwest............ (Common Licorice Fern) *P. glycyrrhiza.*

Fronds 20 to 40 cm long, the blades oblong to somewhat ovate, with segments rounded to somewhat pointed; veins mostly opaque; Sierra Nevada parks. ....*P. californicum.*

Fronds mostly 10 to 24 cm long, the stalks mostly about as long as the blades; leafblades oblong to elliptic, the segments oblong to oval or somewhat spatulate with usually rounded tips; widespread but not common............ (Western Polypody) *P. hesperium.*

OCCURRENCE.—*Polypodium californicum* (*P. vulgare* var. *intermedium*): (K, S); *glycyrrhiza* (*P. vulgare*): (O, MR, Yo); *hesperium* (*P. vulgare* var. *columbianum*): (O, MR, G, RM, Z); *scouleri*: (O).

POLYSTICHUM (Sword Fern, Shield Fern)

KEY TO THE SPECIES

Fronds 30 to 100 (110) cm long; leafblades twice-divided; leaflets narrowly triangular, divided into somewhat oblique elliptic segments with long-awned teeth; indusium with margin irregularly toothed; mostly northwest parks. .... (Anderson's Shield Fern) *P. andersonii.*

Fronds 15 to 60 (180) cm long; leafblades once-divided, or sometimes the leaflets deeply divided at the base only.

Leaflets triangular-ovate to triangular-oblong, deeply lobed or divided at the base and irregularly toothed above, the teeth rather stiff-pointed; indusium thin, irregularly toothed; fronds 15 to 40 cm long............ (Eaton's Shield Fern) *P. scopulinum.*

Leaflets narrowly oblong-lanceolate to linear, tapering to a point, the margins rather unevenly but finely toothed, with broad triangular tooth on upper side at base, not lobed or divided (except sometimes in var. of *P. munitum*).

Leaflet margins with conspicuous spreading spinulose teeth; indusium not toothed or hairy-fringed; fronds mostly 15 to 60 cm long, the stalks very short (1 to 6 cm long); northern Pacific slope

parks and Rocky Mountains. (Holly Fern) *P. lonchitis.*
Leaflet margins sharply double-toothed with rigid incurved teeth (deeply toothed to incised in var. *inciso-serratum*); indusium more or less toothed or hairy-fringed; fronds mostly 30 to 180 cm long (30 to 50 cm in var. *imbricans* and 15 to 20 cm in var *nudatum*), the stalks 5 to 60 cm long; Pacific slope parks. .... (Sword Fern) *P. munitum.*

OCCURRENCE.—*Polystichum andersonii*: (O, MR, G); *lonchitis*: (MR, C, L, G, GT, RM; *munitum* (and varieties): (O, MR, C, L, Yo, K, S); *scopulinum*: (C, L, Yl, GT).

WOODWARDIA (Chain Fern)

OCCURRENCE.—*Woodwardia radicans*: (Yo, K, S).

ASPLENIUM (Spleenwort)

KEY TO THE SPECIES

Fronds slender and grasslike, commonly less than 15 cm long, the stalk much longer than the blade; blade linear, with 2 to 5 linear segments; leafstalk green except at base; southern Rocky Mountains and southwest............*A. septentrionalis.*
Fronds with broader blade, 8 to 25 cm long, the stalk much shorter than the blade; blade with 10 to 60 segments, the segments small, up to about 6 mm long, oval to broadly oblong; found in the northwest and Rocky Mountains but not common.
Leafstalk and main axis dark; margins of segments slightly and shallowly notched, forming broad flat teeth. ....*A. trichomanes.*
Leafstalk and main axis green except becoming brown at base; leaf segments more deeply notched, with broad rounded teeth.........................*A. viride.*

OCCURRENCE.—*Asplenium septentrionalis*: (RM); *trichomanes*: (O, MR, RM); *viride*: (O, MR, G).

ADIANTUM (Maidenhair Fern)

KEY TO THE SPECIES

Leafblades elongate, with one main stem continuous with leafstalk and several short branches, these and the ultimate segments usually spreading in about the same plane; segments roundish or fan-shaped with broad tips.
Fronds lax or drooping; segments of blades irregularly and deeply cut; found in the southwest parks.................(Venus-hair Fern) *A. capillus-veneris.*
Fronds erect; segments of blades shallowly toothed; Pacific coast species, not common in the western parks. (California Maidenhair Fern) *A. jordanii.*
Leafblades roundish to broadly kidney-shaped, composed of 5 to 14 finger-like divisions spreading in the same plane from the upper side of the two branches of the forked leafstalk; main divisions 10 to 30 (40) cm long, with numerous broad, irregularly cleft segments spreading in two rows on opposite sides of the branch; widespread in the western parks. ....
.... (Western Maidenhair Fern) *A. pedatum* var. *aleuticum.*

OCCURRENCE.—*Adiantum capillus-veneris*: (MV, Z, GC); *jordanii*: (C); *pedatum* var. *aleuticum*: (O, MR, C, Yo, S, G, Yl, GT, Z).

CRYPTOGRAMMA (Rock-brake)

KEY TO THE SPECIES

Fronds densely clustered, the fertile 7 to 30 cm long; segments of fertile leafblades linear-oblong; widespread on cliffs and rock slopes in the Pacific slope and Rocky Mountain parks.
Leafstalks light brown to yellowish; segments of fertile leafblades about 6 to 12 mm long, obtuse; found at the higher elevations. ....
....................(American Parsley Fern) *C. crispus* var. *acrostichoides.*

Leafstalks brown and shiny; segments of fertile blades to 15 mm long, tipped with rigid point; found at middle elevations and above. (*Cheilanthes siliquosa, Pellaea densa*). .... *C. densa.*

Fronds more scattered or loosely clustered, the fertile 8 to 20 cm long; segments of fertile blades linear-oblong to lanceolate, up to 2 cm long; found at middle elevations and below; not common. .... *C. stelleri.*

OCCURRENCE.—*Cryptogramma crispus* var. *acrostichoides*: (O, MR, C, L, Yo, K, S, G, Yl, GT, RM); *densa* (*Pellaea densa, Cheilanthes siliquosa*): (O, C, Yo, K, S, G, GT); *stelleri*: (G).

PELLAEA (Cliff Brake)

KEY TO THE SPECIES

Leafblades once-divided, sometimes with lower segments deeply lobed or divided into 3 segments.

Leaflets mostly 2-parted into unequal lobes (mitten-shaped), the veins prominent; leafstalks brittle; somewhat wrinkled as though corrugated; fronds about 5 to 15 cm long, densely tufted; California and Rocky Mountain parks. .... *P. breweri.*

Leaflets not divided or the lower parted into 3 smaller segments, the veins not conspicuous; leafstalks not wrinkled.

Leafblades divided into 5 to 16 pairs of leaflets, these not lobed nor divided, not stalked; band of sporangia bordering fertile segments not concealed by an inrolled margin; leafstalks 4 to 21 cm long; mostly California parks........................ *P. bridgesii.*

Leafblades divided into 3 to 8 pairs of leaflets, the lower 1 or 2 pair usually divided into 3 segments; marginal band of sporangia at least partly concealed by inrolled margin of segments; leafstalks 2 to 6 cm long; southwest parks. .... *P. atropurpurea* var. *simplex.*

Leafblades 2- to 4-times divided.

Leafblades 3- to 4-divided, the segments minute, white-waxy beneath; southwest. .... *P. limitanea.*

Leafblades 2- or 3-divided.

Leaf segments roundish to oval, inrolled at edge of margins only, scarcely covering marginal band of sporangia; scales on underground stems linear, uniformly colored.

Fronds 15 to 75 cm. long; California parks. .... (Coffee Fern) *P. andromedaefolia.*

Fronds 3 to 16 cm long; southwest................................ *P. jonesii.*

Leaf segments narrowly ovate to elliptic or linear, the margins strongly inrolled, tipped with a rigid point; scales on underground stem with a dark opaque stripe and thin border.

Leafblades mostly 3-times divided, at least in the lower part; Sierra Nevada and southwest.

Leaf segments 2 to 6 mm long, the lower smallest divisions in 3's like the foot of a bird............................ ....(Tea Fern, Bird's Foot Fern) *P. mucronata.*

Similar but with segments longer, to 7 mm long.................... .... *P. longimucronata.*

Leafblades 2-times divided; Pacific slope.

Leaflets with 5 to 7 pairs of segments; segments narrowly oblong, shorter than the axis of the leaflets; fronds 12 to 18 cm long. ....*P. compacta.*

Leaflets with 1 to 5 pairs of segments; segments narrowly linear, as long or longer than the axis of the leaflet; fronds 15 to 40 cm long........................ .... *P. brachyptera.*

OCCURRENCE.—*Pellaea andromedaefolia*: (Yo, K, S); *atropurpurea* var. *simplex* (*P. suksdorfiana*): (Z, GC); *brachyptera*: (C, Yo (listed); *breweri*: (Yo, K, S, GT, RM (reported); *bridgesii*: (Yo, K, S); *compacta*: (Yo, S); *densa* (see *Cryptogramma densa*); *jonesii* (*Notholaena jonesii*): (GC); *limitanea* (*N. limitaena*): (GC) (reported); *longimucronata*: (Z, GC); *mucronata* (*P. ornithopus*): (Yo, K, S, Z).

CHEILANTHES (Lace Fern, Lip Fern)

KEY TO THE SPECIES

Leaf segments without scales, merely hairy or woolly (or glabrous); fronds densely tufted from thick, short-creeping underground rhizomes; mostly southwest parks.

- Leafblades broadly triangular-ovate, glabrous, mostly 3-pinnate, with large triangular basal pinnae; leaf segments narrowly pointed; sori solitary at vein tips, with separate roundish-lunate indusium; fronds 6 to 37 cm long. .... *C. californica.*
- Leafblades narrowly oblong to ovate (or triangular-ovate), hairy or woolly, at least below, the segments more or less rounded and with inrolled margins forming a more or less continuous covering over the sori; fronds 5 to 25 cm long.
  - Leafblades mostly 3-pinnate, the segments roundish and bead-like, about 1 to 1.5 mm in diameter, green and sparingly hairy above, coarsely tawny-hairy below. .... *C. feei.*
  - Leafblades mostly 2-pinnate, the segments rounded but shallow, not bead-like, often to 2.5 or 3.5 mm long, densely woolly above and below with whitish or tawny hairs.
    - Grand Canyon National Park. .... *C. parryi.*
    - Sequoia National Park. .... *C. cooperae.*

Leaf segments with scales, at least on the midrib below, essentially glabrous above; fronds loosely or densely clustered from long-creeping rhizomes.

- Leafblades mostly twice-pinnate, the segments mostly oblong, densely cottony beneath; mostly Pacific slope. .... *C. gracillima.*
- Leafblades mostly 3- or 4-pinnate, the segments roundish and bead-like.
  - Scales of leaf segments very finely toothed, not hairy-fringed; mostly southwest. .... *C. fendleri.*
  - Scales of leaf segments fringed with long hairs, at least at base. (The three following forms hardly distinguishable.)
    - Scales with broadly heart-shaped base, the basal lobes overlapping.
      - Leaf segments without scales above, the scales below longer than the segments, whitish to light brown. .... *C. covillei.*
      - Leaf segments with small star-shaped scales above, those below smaller, numerous, dark-colored. .... var. *intertexta.*
    - Scales narrower, merely rounded at base. .... *C. wootonii.*

OCCURRENCE.—*Cheilanthes californica*: (S); *cooperae*: (S); *covillei*: (Z); var. *intertexta*: (K); *feei*: (MV, GC); *fendleri*: (RM); *gracillima*: (O, MR, C, L, Yo, K, S, G); *parryi* (*Notholaena parryi*): (GC); *siliquosa* (see *Cryptogramma densa*); *wootonii*: (GC).

NOTHOLEANA (Cloak Fern)

OCCURRENCE.—*Notholaena sinuata*: (GC).

PTERIDIUM (Bracken)

OCCURRENCE.—*Pteridium aquilinum* var. *pubescens*: (O, MR, C, L, Yo, K, S, G, Yl, GT, RM, Z, GC).

CYSTOPTERIS (Bladder Fern)

KEY TO THE SPECIES

Fronds clustered, the leafstalks shorter than the blades; blades lance-shaped to oblong-lance-shaped, twice- to three-times divided.
Leafblades broadest above the base, those of sterile and fertile fronds similar, without bulblets; veins mostly extending to points of marginal teeth; widespread in the western parks. ....(Fragile Fern) *C. fragilis.*
Leafblades broadest at base, those of fertile fronds mostly narrower than the sterile and tapering to long slender tips; veins mostly ending at notches between the teeth; back of leaf often bearing small roundish bulblets which drop and start new plants; rare, in the Southwest.................................. *C. bulbifera.*
Fronds arising singly, scattered; leafstalks usually much longer than the blades; blades broadly triangular-ovate, 3- to 4-divided; Mt. McKinley National Park...... .... *C. montana.*

OCCURRENCE.—*Cystopteris bulbifera*: (Z); *fragilis*: (MK, O, MR, C, L, Yo, K, S, G, Yl, GT, RM, MV, Z, GC); *montana*: (MK).

WOODSIA (Woodsia)

KEY TO THE SPECIES

Fronds rarely more than 15 cm long, the leafstalks jointed about 1/3 from base; leaf segments hairy and usually scaly on lower surface; indusia extending beyond clusters of sporangia (sori) as 10 to 20 hairlike filaments spreading from underneath; northern species. ....*W. ilvensis.*
Fronds 6 to 25 (or 40) cm long, the leafstalks not jointed to the base; indusia generally hidden by sporangia or the hair-like segments few; widespread in the parks.
Fronds 10 to 40 cm long, hairy on stalk and lower surface of blade with stiff whitish hairs mixed with glands; indusium divided into flat hairlike segments hidden beneath the sporangia; Pacific slope and Rocky Mountain parks. .... *W. scopulina.*
Fronds 6 to 25 cm long, smooth, the blades sometimes glandular or fringed with hairs, not stiff-hairy as above.
Leafblades and stalks smooth; indusium divided into slender segments resembling strings of tiny beads; Rocky Mountain and southwestern parks. ....*W. oregana.*
Leafblades fringed with whitish hairs, otherwise smooth; indusium divided into long hairlike lobes much longer than the sorus; Southwest. ....*W. mexicana.*

OCCURRENCE.—*Woodsia ilvensis*: (MK); *oregana*: (G, Yl, RM, GC); *mexicana*: (GC); *scopulina*: (O, Yo, K, S, G, Yl, RM).

ATHYRIUM (Lady Fern)

KEY TO THE SPECIES

Fronds 20 cm to 1 m long, nearly erect; stalks brittle; sori roundish, with no apparent indusium, except sometimes a few slender rudimentary hair-like segments underneath; widespread in the western parts at upper elevations.............................. (Alpine Lady Fern) *A. alpestre.*
Fronds up to 2 m long, erect-arching; stalks fragile; sori somewhat curved (kidney- to horseshoe-shaped); indusium evident, attached at the inner side, the free edge usually fringed with hairs or fine teeth; a very variable species widespread in the Pacific slope and Rocky Mountain parks. .... (Lady Fern) *A. filix-femina.*

OCCURRENCE.—*Athyrium alpestre* (including var. *americana*): (O, MR, Yo, K, S, G, Yl, GT, RM); *filix-femina*: (O, MR, C, L, Yo, K, S, G, Yl, GT, RM).

DRYOPTERIS (Wood Fern, Shield Fern)

KEY TO THE SPECIES

Leafblades ovate to lanceolate-triangular, widest near base, 2- or 3-times divided.

Fronds scattered, long-stalked, the stalks about as long or longer than the blades; blades characteristically assuming a horizontal position more or less at right angles to stalk, 8 to 25 cm long, about as broad as long, divided into 3 nearly equal stalked divisions, these again 1- or 2-times divided; leafstalks smooth and lustrous except at the straw-colored base; sori small, near the margin, without indusium; Northwest and Rocky Mountains. (*D. linnaeana*).. (Oak Fern) *D. disjuncta.*

Fronds clustered, erect or spreading, short-stalked, the stalks shorter than the blades, scaly; leafblades 15 to 45 or 90 cm long, much longer than wide, the segments with branch-veinlets ending in spine-tipped teeth; indusium evident.

Leafblades mostly 2- to 3-times divided; indusium fragile, flat, soon curling back.

Leaf-segments flat, glabrous on lower surface (not glandular); sori terminal on veinlet tips, with indusia not glandular; scales of leafstalk and axis uniformly pale brownish; southwest and Rocky Mountains.........*D. spinulosa.*

Leaf-segments concave, somewhat glandular on lower surface; sori a little back from ends of veinlets, with indusia often sparsely glandular; scales dark brownish, especially in center; northwest. (*D. austriaca*).............*D. dilatata.*

Leafblades 2-times divided; indusium firm, strongly convex, with glandular margins; California parks. ....*D. arguta.*

Leafblades lanceolate to elliptic or reverse-lanceolate, narrowed toward base, twice-divided, the lowest leaflets usually shorter than the middle ones; fronds clustered; segments not spine-toothed.

Leafblades small, 7.5 to 30 cm long, the stalk and main axis commonly conspicuously scaly; sori large, covered by large nearly orbicular long-persistent indusia, often so close together as to appear as overlapping scales; indusium margins usually ragged and sparingly glandular; plants fragrant; Mt. McKinley National Park............*D. fragrans.*

Leafblades larger, 10 to 100 (120) cm long, the stalk and main axis smooth or scaly.

Margins of leaf-segments not toothed; leafstalks much shorter than blade, straw-colored, nearly smooth or naked; sori near the margins, the indusia very small, long-hairy, glandular; northwest (*D. nevadensis*) .... *D. oregana.*

Margins of leaf-segments toothed; leafstalks scaly with pale brown scales; sori nearly medial or closer to midrib than margins, large, the indusia orbicular, smooth.

Leafstalks short or long, to 50 cm long, with ovate to broadly lanceolate scales; sori not confined to basal half of segments; indusia flat, thin; northern Rocky Mountains. .... *D. cristata.*

Leafstalks shorter than blades, 2 to 10 (25) cm long, with narrowly lanceolate to linear scales; sori mostly on basal half of segments; indusia convex, firm; widespread................ .... (Male Fern) *D. filix-mas.*

OCCURRENCE.—*Dryopteris arguta*: (Yo, K, S); *cristata*: (G); *dilatata* (*D. austriaca*): (MK, O, MR); *disjuncta* (*D. linnaeana*): (MK, O, MR, G, GT, RM); *filix-mas*: (MR, G, Z); *fragrans*: (MK); *oregana*: (MR); *spinulosa*: (RM, MV).

PITYROGRAMMA (Gold Fern)

OCCURRENCE.—*Pityrogramma triangularis*: (O, MR); var. *pallida*: (Yo, K, S).

MARSILEACEAE—Pepperwort Family
MARSILEA (Pepperwort)

OCCURRENCE.—*Marsilea oligospora*: (Yl, GT).

SALVINIACEAE—Salvinia Family
AZOLLA (Water Fern)

OCCURRENCE.—*Azolla filiculoides*: (S).

EQUISETACEAE—Horsetail Family
EQUISETUM (Horsetail, Scouring Rush)

KEY TO THE SPECIES

Stems slender, less than 3 mm in diameter, mostly less than 75 cm high, with central cavity none or less than half the diameter of the stem.

- Stems tufted, evergreen, not branched; sheaths at joints of stem with bristle-like teeth; northern species.
  - Stems 15 to 45 (55) cm high; sheaths 5- to 10-toothed, the teeth soon falling. .... *E. variegatum.*
  - Stems about 7 to 15 cm high; sheaths 3-toothed, the teeth persistent. .... *E. scirpoides.*
- Stems scattered or clustered, annual, at least some of them branched; sheaths with lance-shaped persistent teeth.
  - Stems all alike, the fertile as well as the sterile branched before cones mature; branches few, simple, hollow, 4- to 7-angled, the sheaths with as many teeth, the teeth usually white-margined; northern species. .... *E. palustre.*
  - Stems of two kinds, the sterile branched, the fertile at least at first unbranched or becoming branched after maturity of the cones; branches solid.
    - Fertile stems becoming branched; northern species not common in parks.
      - Branches freely again branched, the branchlets with 3-toothed sheaths, the teeth brownish.......... *E. sylvaticum.*
      - Branches simple, rather short, 3 (rarely 4 or 5)-angled, the sheaths mostly 3-toothed. ....*E. pratense.*
    - Fertile stems not branched, soon withering, the sheaths whitish-papery with about 12 brown pointed teeth; branches of sterile stem mostly simple, 4-(rarely 3)-angled, the sheaths usually 4-toothed; widespread species common in the western parks ....*E. arvense*

Stems mostly 3 mm or more in diameter, usually averaging higher, up to 90 cm or more, the central cavity at least $\frac{1}{2}$ the diameter of the stem.

- Fertile and sterile stems similar, all unbranched or the branches relatively sparse; cones mostly 1 to 2 cm long, not larger.
  - Stems annual, the sheaths with persistent teeth; northwestern parks.
    - Stems branched, the branches of two kinds, some 4-angled and hollow, some 3-angled and solid, the sheaths loose, with membranous-margined herbaceous teeth; cones small with poorly developed spores; stems with central cavity $\frac{1}{2}$ to $\frac{2}{3}$ diameter of stem. (Considered a hybrid, *E. arvense* × *E. limosum*)..........*E. litorale*
    - Stems branched or unbranched, the branches 4- or 5-angled, hollow; sheaths appressed, with dark brown rigid teeth; cones 1 to 2 cm long, short-stalked, the spores well developed; stems with large central cavity (*E. fluviatile*) .... *E. limosum*

Stems annual or perennial, usually all unbranched at least at first, the sheaths with teeth usually falling relatively early from body of sheath.

Stems easily compressed, smooth, 15- to 30-grooved, 30 to 90 cm high, usually annual; sheaths somewhat funnel-shaped, usually with a single dark band at base of teeth, the teeth also blackish; cone with rounded teeth; widespread in the parks. (*E. laevigatum*, in part).. *E. kansanum*

Stems firm, roughish with rows of small tubercles on the ridges, 8 to 34 (or 48)-grooved, 50 to 120 (300) cm high; sheaths cylindric, commonly with two dark bands, one at base of teeth and one below; cone usually tipped with a firm dark point; Eurasian species *E. hyemale*

Stems 50 to 300 cm high, the ridges with a single row of tubercles; northern Rocky Mountains. (*E. praealtum*, as to ours).....................var. *robustum*

Stems 50 to 120 (150) cm high, the ridges with 2 indistinct rows of tubercles; Pacific slope parks.. var. *californicum*

Fertile stems whitish, succulent, with loose sheaths often longer than the stem sections, the whole stem soon withering after maturing of spores; cones 2.5 to 8 cm long; sterile stems with numerous branches at the joints; branches 7 to 15 cm long, deeply grooved with about 10 very rough ridges extending into the sheaths and ending in pairs in the 5 teeth of the sheath; rare, in the northwest................*E. telmateia* var. *braunii*

OCCURRENCE.—*Equisetum arvense*: (MK, O, MR, C, L, K, S, G, Yl, RM, Z, GC); *hyemale* var. *californicum*: (O, MR, C, Yo, K, S, G); var. *robustum* (*E. praealtum*): (G, Yl, RM); *kansanum* (*E. laevigatum*): (S, G, Yl, RM, B, Z, GC); *limosum* (*E. fluviatile*): (MK, O, MR, G); *litorale*: (G); *palustre*: (MK, MR, G); *pratense*: (GT); *scirpoides*: (MK, G); *sylvaticum*: (MK, G); *telmateia* var. *braunii*: (O, MR); *variegatum*: (G, Yl).

LYCOPODIACEAE—Clubmoss Family

LYCOPODIUM (Clubmoss)

KEY TO THE SPECIES

Erect or ascending branches freely branched, clothed with scale-like or awl-shaped leaves in 4 (or 6) rows, the leaves of 2 or 3 kinds, closely appressed to the stems, at least some of the branches tending to be flattened.

Main stems creeping underground, the erect branches distinctly treelike with forking branchlets spreading from a simple trunk-like basal part; cones 1.5 to 6.5 (8.5) cm long, borne singly at the tips of branches, not stalked. .... (Ground Pine) *L. obscurum*

Main stems running on or slightly below surface of the ground, the erect branches with branchlets rather crowded, tufted or somewhat fan-like or tree-like.

Branchlets distinctly flattened, in rather fan-like arrangement; cones 1 to 3 cm long, borne singly or several (2 to 5) at the top of a scaly erect stalk terminating a leafy branch, the stalk (0.5) 3 to 6 cm long. ....(Ground Cedar) *L. complanatum*

Branchlets somewhat tufted, the sterile somewhat flattened, the fertile more or less cylindric; cones 0.6 to 2 cm long, borne singly at the ends of the branches, not stalked. ....(Alpine Clubmoss, Ground Fir) *L. alpinum*

Erect or ascending branches numerous along the creeping stems, not much branched; leaves of one kind, needle-like, thickish, not tightly appressed to the stems (somewhat appressed at base in *L. sitchense*).

Leaves 4- or 5-ranked, short, less than 5 mm long, the base somewhat appressed to the stem; cones 0.5 to 2 cm long, borne singly directly at the tips of the branches or on short stalks up to 1 cm long. ....(Sitka Clubmoss) *L. sitchense*

Leaves many-ranked, crowded, spreading or ascending, mostly about 2.5 to 10 mm long.

Leaves relatively soft, at first tipped by a soft hair-like bristle; cones 1.5 to 10 (15) cm long, on scaly stalks.

Cones generally 2 to 6 at the end of a stalk, the stalks 3 to 15 cm long; leaves usually spreading.. (Running pine) *L. clavatum*

Cones borne singly on stalks 0.5 to 2.5 cm long; leaves usually ascending rather close to the stem.....var. *monostachyon*

Leaves rigid, often sharp-pointed; cones not stalked or short-stalked, or sporangia borne in axils of upper leaves.

Sporangia borne in cone-like structures terminating the branches; cones not stalked or on short stalks up to about 1 cm long, borne singly.....(Stiff Clubmoss) *L. annotinum*

Sporangia borne in the axils of the upper foliage leaves; not in special cone-like structures; leaves pale green or yellowish, shining. (Fir Clubmoss, Mountain Clubmoss) *L. selago*

OCCURRENCE.—*Lycopodium alpinum*: (MK, G); *annotinum* (including var. *pungens*); (MK, MR, G, YI, RM); *clavatum* (including var. *monostachyon*): (MK, O, MR, G); *complanatum*: (MK, MR, G); *obscurum*: (G); *selago*: (MK, O, MR, G, RM); *sitchense*: (O, MR).

SELAGINELLACEAE—Spikemoss Family

SELAGINELLA (Spikemoss)

KEY TO THE SPECIES

Plants lax, the stems loosely branched.

Plants usually with long branches hanging from trees in humid forests; leaves bright green, slender lance-shaped with long base (up to 1 mm), closely appressed to the stem, tipped with yellowish bristle-like awn less than 0.3 mm long; found in coastal northwest. ....*S. oregana*

Plants with prostrate stems 5 to 15 cm long, rooting throughout their length, with numerous more or less ascending branches forming loose mats; leaves oblong-linear, the basal attachment short, tipped with a whitish bristle-like awn.

Leaves with awn-tips 0.3 to 2 mm long, the hair-like cilia on margins relatively few or wanting; plants bright green; found in the southwest. .... *S. underwoodii*

Leaves with awn-tips not exceeding 0.3 mm long, the marginal hair-like cilia 10 to 18 on each side; plants pale green; found in the northwest. ....*W. wallacei*

Plants usually forming dense mats, the stems prostrate with short congested branches.

Leaves only 1 mm long, blunt-pointed, terminal awn absent or very short; found in southern Rocky Mountains and southwest. ....*S. mutica*

Leaves mostly nearly 2 mm long or longer, tipped with evident bristle-like awn.

Leaves 1.8 to 2.5 mm long, the awns rigid, yellowish.

Leaves with 10 to 14 marginal hairs (cilia) on each side; fertile spikes about 1 cm long or slightly less; found in northern Rocky Mountains. ....*S. standleyi*

Leaves with 2 to 7 marginal hairs (cilia) on each side, these confined to lower half, soon falling; fertile spikes 1 to 2.5 cm long; found in Sierra Nevada parks. *S. watsoni*

Leaves 2 to 3.5 mm long, the awns stiff, white-membranous at least at the tips.

Awns 0.6 to 1.5 mm long, very conspicuous at tips of branches where leaves are crowded together in tufts; marginal cilia 5 to 12 (16) on each side.

Awns to 1.5 mm long; spikes 1 to 3 cm long; most common species in Rocky Mountian parks..... *S. densa*

Awns to 1 mm long; spikes 0.5 to 1 cm long; Sierra Nevada. .... *S. hanseni*

Awns 0.3 to 0.6 mm long; leaves with marginal cilia 4 to 9 on each side; spikes 1 to 2.5 (3) cm long. (Includes *S. montanensis* of Flora of Glacier Park). *S. scopulorum*

OCCURRENCE.—*Selaginella densa*: (G, Yl, GT, RM); *hansenii*: (K); *mutica*: (RM, Z, GC); *oregana*: (O); *scopulorum*: (O, G); *standleyi*: (G); *underwoodii*: (GC); *wallacei* (*S. rupestris* as to ours): (O, MR, G); *watsonii*: (Yo, K, S).

ISOETACEAE—Quillwort Family

ISOETES (Quillwort)

KEY TO THE SPECIES

Leaves submersed or rarely emersed, without stomata; peripheral fibrous strands lacking; ligule short-triangular; megaspores marked all over with distinct or confluent crests, forming an irregular network on basal face; Rocky Mountain parks.

Sporangia orbicular or broadly elliptic, 3 to 5 mm long, the vellum narrow; megaspores 0.6 to 0.8 mm in diameter; microspores smooth or papillose (has been confused with *I. lacustris of the* Old World)........................ .... *I. macrospora*

Sporangia nearly orbicular, 5 to 6 mm long, about 1/3 covered with the vellum; megaspores 0.5 to 0.65 mm in diameter; microspores spinulose (*I. lacustris* var. *paupercula*) ....*I. occidentalis*

Leaves submersed or terrestrial, with or without stomata and peripheral fibrous strands; megaspores smoothish or marked with spines or tubercles which may be confluent into short ridges; Pacific slope parks.

Megaspores smoothish or obscurely marked with low tubercles or wrinkles; microspores smooth to slightly spinulose; sporangia about 1/3 or less covered by the vellum.

Leaves submersed or emersed, the stomata numerous; peripheral strands usually 4; ligule narrowly elongate-triangular; sporangia orbicular to oblong, 3 to 6 mm long; megaspores 0.4 to 0.52 mm in diameter. ....*I. howellii*

Leaves submersed most of the time; stomata few or lacking; peripheral strands usually lacking; ligule short-triangular.

Sporangia 3 to 4 mm long; megaspores 0.3 to 0.45 mm in diameter; leaves 6 to 13 (25) cm long, submersed in shallow water. ....*I. bolanderi*

Sporangia small; megaspores 0.4 to 0.52 mm in diameter; leaves 2 to 3 cm long, deeply submersed. ....*I. pygmaea*

Megaspores marked with spines or tubercles, these often confluent into short ridges; microspores smooth to slightly roughened or papillose; sporangia orbicular to broadly elliptic; leaves lacking peripheral strands; stomata few or none; ligule short-triangular; northwest parks.

Leaves 3 to 10 (15) cm long; sporangia 4 to 5 mm long, 1/5 to 2/3 covered by velum; megaspores 0.5 to 0.8 mm in diameter, marked with points or tubercles. ....*I. piperi*

Leaves 8 to 25 cm long; sporangia 3 to 5 mm long, 1/2 to 3/4 covered by velum; megaspores 0.4 to 0.56 mm in diameter, spinose. (*I. braunii*). .... *I. muricata*

OCCURRENCE.—*Isoetes bolanderi*: (MR, Yo, K, S, Yl); *howellii*: (S); *macrospora*: (Yl); *muricata* (*I. braunii*): (O, MR, C); *occidentalis* (*I. lacustris* var. *paupercula*): (Yl, RM); *piperi*: (O); *pygmaea*: (Yo, K).

Spermatophyta. Seed Plants.

GYMNOSPERMAE (Gymnosperms)

Leaves needle-like, linear, awl-shaped, or scale-like (or apparently none in Ephedra); seeds borne naked on woody or membranous scales, forming cones, or in fleshy berry-like fruits; mostly evergreen trees or shrubs.

KEY TO THE FAMILIES AND GENERA

Leaves needle-like or linear; seeds borne in pairs on the scales of woody cones; forest trees. Family PINACEAE, except as noted.

Leaves in clusters of 2 or more, or if single, the base surrounded by sheath of tawny membranous bracts (fascicled).

Leaves in fascicles (groups of 2, 3, or 5, or 1, with basal sheath of membranous bracts); cone scales more or less thickened towards tips, with scale-like bracts on lower side very short and not showing between cone scales; evergreen trees widespread in western parks. .... (Pines) PINUS, p. 26

Leaves borne in clusters of several to many on short peg-like branchlets; cone scales thinnish, often with long pointed bracts extending from between the scales; deciduous trees (losing their leaves during the winter); trees often favor low and swampy ground; northern Rocky Mountains and Alaska. .... (Larch, Tamarack) LARIX, p. 28

Leaves borne singly along the branches; cone scales thinnish, with or without protruding bracts (or fleshy or berry-like); evergreen trees (or shrubs).

Generally straight trees with stiffly erect leader at the top and horizontally spreading branches; young bark smooth, marked by smooth round leaf scars; leaves generally blunt (or notched) at tips, spreading in one plane from opposite sides of the stem or curving upwards; cones borne erect on upper branches and falling apart on the tree. ....(Fir) ABIES, p. 28

Mostly straight trees with straight or flexuous nodding leader at top and slender horizontal or somewhat drooping branches (or many-stemmed shrubs); young bark more or less marked by persistent leaf bases; leaves spreading in one plane (with sometimes a shorter row overlying the longer) or more or less spreading from all sides of the twigs; cones (or fleshy fruits) spreading or hanging downward, from outer parts of branches, the cone scales persistent and falling as a unit.

Forest trees (15) 25 to 70 m high.

Leaves mostly less than 2.5 cm long, sometimes sharp-pointed, but the tips not stiffly sharp-pointed with long rigid points; cones with closely overlapping scales; rather widespread trees in the western parks.

Leaves somewhat sharp-pointed at tips, more or less 4-sided in cross-section; twigs roughened by short persistent peg-like leaf bases; cones elliptic to oblong, 2.5 to 10 cm long. ....(Spruce) PICEA, p. 29

Leaves blunt-pointed or somewhat notched at tips, generally flattened or somewhat thickish, but not 4-angled; twigs not roughened, but often marked by leafbases extending somewhat down the stems; cones oval to oblong, small or to 10 cm long; widespread and abundant, especially in parks of the northwest.

Leaves 2 to 3 cm long, more or less spreading from all sides of the stems; cones pendent from near ends of somewhat drooping branches, 5 to 7 (10) cm long, with prominent 3-pointed bracts extending from between the cone scales; leader at top of tree slender, erect. (Douglas Fir) PSEUDOTSUGA, ... p. 30

Leaves 0.5 to 2 cm long, often unequal in length, spreading in two ranks from opposite sides of the stems, the shorter overlying the longer; cones spreading or pendent, 2 to 2.5 or 7.5 cm long, without protruding bracts; slender leader at top of tree nodding. ....(Hemlock) TSUGA, p. 30

Leaves 2.5 to 7.5 cm long, tipped with very sharp rigid points; fruits fleshy, plum-like, 2.5 to 3.5 cm long; in California parks, rare. Family TAXACEAE. ....(California Nutmeg) TORREYA, p. 30

Low or tall, usually many-stemmed shrubs; fruits fleshy berries.

Mostly erect shrubs 1 to 4 m high in our area (or becoming a small tree to about 15 m high in mild humid coastal regions); leaves 1 to 2 cm long, soft-pointed at tips, 2-ranked; berries generally less than 1 cm long, in form of a fleshy red cup containing a single light straw-colored seed; common in the more northern parks. Family TAXACEAE. .... (Yew) TAXUS, p. 30

Spreading shrubs to 1 m high; leaves sharp-pointed, 0.6 to 1.5 cm long, not 2-ranked; berries globose, the seeds completely enclosed by the flesh, dark blue with a powdery film; widespread in western parks. Family CUPRESSACEAE. ....(Ground Juniper) *Juniperus communis* var. *saxatilis*, ... p. 31

Leaves awl-shaped or scale-like, closely covering the twigs (or distant and inconspicuous in *Ephedra*); seeds borne in cones or the fruits fleshy berries.

Leaves closely appressed and overlapping on the twigs, in opposite pairs or spirally arranged on the twigs; stems not distinctly jointed; cones with small flattened laterally winged seeds, or the seeds thickened and wingless in the berries of *Juniperus;* mostly trees (or shrubs).

Leafy twigs rounded and cord-like, not forming flattened sprays.

Leaves somewhat short, awl-shaped, with pointed tips more or less spreading; cones egg-shaped or oval, 4 to 8 cm long; cone scales much thickened at the tips, attached by narrow base; seeds many per scale; large trees to 100 (or more) m high; trunks 1.5 to 10 (12) m in diameter, the bark thick, ridged; found in isolated groves in Sierra Nevada forests at middle elevations between 6,000 and 7,500 feet. Family TAXODIACEAE............. ....(Bigtree, Giant Sequoia) SEQUOIA, p. 30

Leaves scale-like, the tips broad-pointed, not spreading; cones fleshy, berry-like, mostly less than 1 cm in diameter, bluish or becoming somewhat reddish-brown; small trees 10 to 15 (20) m high (or depressed shrubs), with thin shreddy bark; found mostly in Sierra Nevada, Rocky

Mountain, and southwest parks. Family CUPRESSACEAE.....(Cedars and Junipers) JUNIPERUS, p. 31

Leafy twigs more or less flattened, tending to form flattened sprays; forest trees of Pacific slope (and west of Continental Divide in northern Rocky Mountains). Family CUPRESSACEAE.

Cones globose, to 1.2 cm in diameter, composed of 4 to 6 umbrella-shaped cone scales attached by narrowed stalk to central core; trees to 30 or 40 m high; found in the northwest at somewhat higher elevations than the *Thuja* (upper Transition and Canadian Zones)........ ....(Alaska Cedar) CHAMAECYPARIS, p. 31

Cones oblong, composed of thinnish oblong scales which finally spread open to free the seeds; trees of middle elevations (Transition Zone forests).

Trees to 50 m high, with trunks to 3 or 3.5 m in diameter; cones 2 to 2.5 cm long, composed of 6 scales, pendent from near ends of branches; found in middle and southern Cascades and Sierra Nevada..... (Incense Cedar) LIBOCEDRUS, p. 31

Trees to 60 or 70 m high, with trunks to 5 m in diameter; cones 1 to 1.5 cm long, composed of 8 to 12 scales; found in parks of the northwest (including west side of Glacier National Park). ....(Western Red Cedar) THUJA, p. 31

Leaves scale-like, borne in opposite pairs or in 3's at the rather distant nodes; stamens and seeds borne, usually on separate plants, in small cone-like structures in the leaf axils; seeds thickened, ovoid, wingless, pointed or beaked at the tips; apparently leafless desert shrubs with broom-like clusters of branches or the branches more open and spreading; southwest. Family GNETACEAE.. .... (Joint-fir, Mormon Tea) EPHEDRA, p. 31

PINACEAE—Pine Family

PINUS (Pine)

KEY TO THE SPECIES

Needles 1, 2, or 3 in a bundle.

Needles 1 or 2 in a bundle, 2.5 to 5 cm long; cones ovate to somewhat globose, 3 to 5.5 cm long.

Low, round-topped trees 4 to 10 (15) m high with trunks branched from below, the foliage gray-green; cones not stalked, broadly ovate to roundish, with comparatively few large scales; nut pines, the seeds large, thickish, about 1 to 1.5 cm long, wingless as they fall from the cones; characteristic trees in the lower forest zone in the southwest desert country.

Needles one in a bundle; mostly southwest (rare in the Sierra Nevada). ....(Singleleaf Piñon) *P. monophylla*

Needles 2 in a bundle; southwest parks. ....(Piñon Pine) *P. edulis*

Usually slender trees; needles in 2's; cones egg-shaped or somewhat unequal-sided, the scales more numerous, rather thinnish, with prickles at the tips, sometimes remaining attached to stems for many seasons; seeds small, flattish, less than 0.5 cm long, with wings 8 to 12 mm long.. ....(Lodgepole Pine) *P. contorta*

Scrubby trees to about 10 m high; foliage dark green; needles 3 to 4 cm long; cones very unsymmetrical due to cone scales being larger and more thickened on one side than the other; northwest parks. ....(Scrub Pine) var. *contorta*

Slender, generally straight-stemmed trees 15 to 30 (50) m high;

foliage lighter green, the needles averaging longer, about 5 cm long; cones more symmetrical; further south and inland, Sierra Nevada and Rocky Mountains. (*P. murrayana*). ....(Lodgepole Pine) var. *latifolia*

Needles 3 in a bundle (sometimes 2 in *P. ponderosa*), 8 to 25 (30) cm long; cones 5 to 25 (30) cm long.

Rather small trees, to 15 (35) m high with open crowns; bark dark brown, with low broad ridges and scales; cones usually remaining on the trees for many seasons; rare in the foothills below the main forest belt in Yosemite National Park.

Foliage pale yellow-green; needles 8 to 17 cm long; cones short-stalked, 7 to 15 cm long, narrowly ovate and unsymmetrical due to thickened knob-like cone scales on one side, remaining closed and attached to old stems for many years; seeds small, about 0.6 cm. long, with narrow wings to 3.5 mm long. .... (Knobcone Pine) *P. attenuata*

Foliage gray-green; needles 15 to 30 cm long; cones long-stalked, more or less broadly ovate, 15 to 25 cm long; the scales tipped with stout spur-like projections 2 to 2.5 cm long; seeds about 2 cm long, with narrow wing about 0.8 cm wide at tip; a nut pine..(Digger Pine) *P. sabiniana*

Generally tall trees 30 to 60 (75) m high with one main trunk; bark cinnamon- or reddish-brown, broken into irregular plates; needles 12 to 25 cm long; cones short-stalked, oval; yellow pines.

Foliage bright yellow-green; branchlets often somewhat orange-color, not whitish on surface; bark scales sulphur-yellow on under side; cones 7 to 15 cm long; trees forming open, park-like forests in arid Transition Zone; widespread in western parks.........(Ponderosa Pine) *P. ponderosa*

Foliage dull blue-green; branchlets usually whitish on surface; bark scales reddish-brown on under side; cones 12 to 25 (30) cm long; characteristic trees in forest belt just above ponderosa pine, in upper Transition and Canadian Zones of Sierra Nevada.. (Jeffrey Pine) *P. jeffreyi*

Needles 5 in a bundle.

Needles 5 to 10 cm long; cones cylindric, long-stalked and pendent from the ends of the branches; generally rather large handsome trees 30 or more m high; middle altitudes.

Slender trees 30 to 50 m high, generally found in upper or Canadian Zone forests; cones 10 to 20 cm long; widespread in Pacific slope parks and occasionally in northern Rocky Mountains west of Continental Divide. ......(Western White Pine) *P. monticola*

Large trees reaching 75 m in height; cones 20 to 40 (55) cm long; southern Cascades and Sierra Nevada parks, generally in Transition Zone forests. ....(Sugar Pine) *P. lambertiana*

Needles generally shorter, 2 to 7 cm long; cones ovate or globose to oblong, short-stalked or nearly unstalked, spreading from near ends of branches; small trees usually less than 25 m high; generally found at higher altitudes.

Needles 3.5 to 7.5 cm long; cone scales without prickles but sometimes with stout point; Pacific slope and Rocky Mountain parks.

Cones oval to somewhat cylindric, 8 to 20 cm long, light brown, the scales rather thinnish and opening at maturity; Rocky Mountains (and southern Sierra Nevada)....... .... (Limber Pine) *P. flexilis*

Cones ovate to nearly globose, 3.5 to 7.5 cm long, purple, the scales

thickened at tips and remaining closed for some time after maturity; Pacific slope and Rocky Mountain parks (except southern).. (Whitebark Pine) *P. albicaulis*

Needles 2.5 to 3.5 cm long; cones ovoid, the scales thickened at tips, armed with a slender prickle; trees of limited distribution.

Cones 3.5 to 7.5 cm long, dark reddish-brown, the prickles very small; southern Sierra Nevada parks. ....(Foxtail Pine) *P. balfouriana*

Cones 7 to 9 cm long, dark purplish-brown, the prickles about 6 mm long; southwest. ....(Bristlecone Pine) *P. aristata*

OCCURRENCE.—*Pinus albicaulis*: (O, MR, C, L, Yo, K, S, G, Yl, GT); *attenuata*: (Yo); *aristata*: (B); *balfouriana*: (K, S); *contorta*: (O, MR); var. *latifolia*: (C, L, Yo, K, S, G, Yl, GT, RM); *edulis*: (MV, B, Z, GC); *flexilis*: (S, G, Yl, GT, RM); *jeffreyi*: (L, Yo, K, S); *lambertiana*: (C, L, Yo, K, S); *monophylla*: (Yo, K, S, B, Z, GC); *monticola*: (O, MR, C, L, Yo, K, S, G); *ponderosa*: (O (rare) MR (rare), C, Yo, S, G (rare), M, MV, B, Z, GC); *subiniana*: (Yo).

LARIX (Larch, Tamarack)

KEY TO THE SPECIES

Straight-trunked trees to about 20 m high with narrow crown; twigs glabrous; needles 1.5 to 2.5 cm long, 3-sided; cones ovoid, small, about 1.5 to 2 cm long, without protruding bracts between the cone scales; moist or swampy areas in far north and across northern part of North America. ....(Eastern Larch, American Larch) *L. laricina*

Large or small trees; twigs hairy, at least at first; needles 3 to 5 cm long; cones oblong, with long, slender-pointed bracts protruding from between the cone scales; northern Rocky Mountains, not common.

Tall straight trees to 60 (80) m high with long tapering trunks and sparse crown; needles 3 to 5 cm long, 3-sided; cones 2.5 to 4 cm long; found at lower elevations, below 7,000 feet. ....(Western Larch) *L. occidentalis*

Small trees 7 to 15 m high with irregularly developed branches; needles 3 to 4 cm long, 4-sided; cones 4 to 5 cm long; found at high elevations, above 7,000 feet. ....(Subalpine Larch) *L. lyallii*

OCCURRENCE.—*Larix laricina*: (MK); *lyallii*: (G); *occidentalis*: (G).

ABIES (Fir)

KEY TO THE SPECIES

Trees occurring from middle Cascades south to the southern Sierra Nevada and in the southwest; leaves flattened or more or less ridged down the middle above and below (with raised midrib); forest trees to 60 (80) m high.

Leaves (3.5) 4 to 7 cm long, about 3 mm wide, those on lower part of tree more or less flattened; foliage dull green; branchlets glabrous and shining; inner bark buff colored; cones oblong, 7 to 12 cm long, without bracts protruding from between the scales; commonly found in the lower or arid Transition Zone forests. .... (White Fir) *A. concolor*

Leaves 2 to 3.5 cm long, more or less equally 4-sided (squarish in cross-section); foliage at first whitish, becoming blue-green; branchlets finely pubescent the first year, becoming glabrous; inner bark deep reddish; cones oblong-cylindric, 15 to 20 cm long; forest trees generally replacing the white fir at upper elevations (Canadian Zone).

Cones without bracts protruding from between cone scales.. (California Red Fir) *A. magnifica*

Cones with bracts protruding from between cone scales and folding backwards towards base of cone. ....(Shasta Fir) var. *shastensis*

Trees occurring in the Northwest and Rocky Mountains; leaves grooved down the middle on upper surface; leaves 2 to 3.5 (5) cm long.

Rather broad-topped trees to 60 (or 90) m high; mostly Canadian Zone forests.

Large trees to 85 (90) m high; leaves dark green above, silvery white below; cones narrowly oblong to narrowly cylindric, the scales without protruding bracts.

Leaves about equal in length, 3 to 5 cm long, about 3 mm wide, spreading opposite each other and tending to form flat sprays; branchlets becoming glabrous the second year; cones green, narrowly oblong, 12 to 18 cm long.. (Lowland White Fir) *A. grandis*

Leaves 2 to 3 cm long, about 1.5 to 2 mm wide, tending to be in 2 series of unequal length and curving upwards; branchlets finely pubescent for many years; cones purple, narrowly cylindric, 9 to 15 cm long. .... (Silver Fir, Lovely Fir) *A. amabilis*

Generally smaller trees 35 to 50 m high (or to 80 m); leaves blue-green; branchlets remaining finely hairy for several years; cones oblong-cylindric, 10 to 20 (25) cm long, with conspicuous protruding bracts turning backwards over cone scales as in Shasta Fir; extending into upper Canadian and Hudsonian Zones; not common. (*A. nobilis* Lindl., not Dietr.)... (Noble Fir) *A. procera*

Slender trees 25 to 40 (60) m high with spire-like tops; cones dark purple, oblong-cylindric, 6 to 10 cm long; branchlets usually rusty-pubescent for several years; widely distributed in the northwest and Rocky Mountains at higher elevations up to timberline, where the trees may be dwarfed and shrub-like..............................(Alpine Fir) *A. lasiocarpa*

OCCURRENCE.—*Abies amabilis*: (O, MR); *concolor*: (C, L, Yo, S, B, Z, GC); *grandis*: (O, MR, G); *lasiocarpa*: (O, MR, C, G, Yl, GT, RM, GC); *magnifica*: (L, Yo, K); var. *shastensis*: (C, S); *procera* (*A. nobilis*): (MR).

PICEA (Spruce)

KEY TO THE SPECIES

Leaves flattened, 1.5 to 2.5 cm long, with white lines of stomata on upper surface only; bark dark reddish- or purplish-brown; branchlets glabrous; winter buds light brown, resinous; cones narrowly oblong-oval, 6 to 10 cm long, yellowish- or reddish-brown, the scales stiff, rounded and irregularly toothed; trees to 35 (or 70) m high, limited in distribution to the humid Pacific coastal forests. .... (Sitka Spruce) *P. sitchensis*

Leaves 4-sided, with white lines of stomata on all sides; trees more widespread in the western parks; winter buds not resinous; cone scales flexuous (except *P. mariana*).

Branchlets glabrous; bark light brown or grayish; cones light brown and glossy, with more or less flexuous scales; trees to about 50 m high.

Leaves rigid, spine-tipped, 1.8 to 2.5 cm long; winter buds light yellowish-brown, long-pointed, with long-pointed scales; cones cylindric-oblong, 5 to 10 cm long, the scales rounded and irregularly toothed at tips; trees found mostly in southern Rocky Mountains and upper-elevation forests of southwest.. (Colorado Blue Spruce) *P. pungens*

Leaves stiffish, sharp-pointed, not rigid, 0.8 to 2 cm long; winter buds blunt-pointed, with loosely overlapping scales; cones to about 5 cm long, the scales rounded at tips, not toothed; trees found generally farther north.

Bud scales notched at tips; cones to 5 cm long; far north, as to our area. .... (White Spruce) *P. glauca*

Bud scales not notched at tips; stems with more prominent persistent leaf stalks than the species; cones somewhat shorter

and scales stiffer; northern Rocky Mountains. .... var. *albertiana*

Branchlets finely pubescent; bark brownish-gray to gray-brown.

Leaves 2.5 to 3 cm long, soft and flexible; cones cylindric-oblong, 5 to 7.5 cm long, light brown and shining, falling from trees at maturity; cone scales flexuous, narrowed and irregularly toothed towards tip; winter buds brownish-yellow, the scales not persistent; forest trees to about 50 m high; most abundant in Rocky Mountain parks, but occurring also in the northwest and at high elevations in the southwest.......................(Engelmann Spruce) *P. engelmannii*

Leaves 0.6 to 1.8 cm long, thickish; cones ovoid, 1 to 3 cm long, purple, becoming grayish-brown, persistent on trees for many years; cone scales stiff, rounded and somewhat toothed at tips; winter buds finely hairy; generally low trees 6 to 10 (30) m high, or often scrubby and only a meter or less; the characteristic tree of northern bogs, wet flats or lake margins....................... (Black Spruce) *P. mariana*

OCCURRENCE: *Picea engelmannii*: (MR, C, G, Yl, GT, RM, GC); *glauca*: (MK); var. *albertiana*: (G); *mariana*: (MK); *pungens*: (GT (rare), RM, B, GC); *sitchensis*: (O, MR).

PSEUDOTSUGA (Douglas Fir)

KEY TO VARIETY

Trees to 60 or 80 m high; leaves dark yellow-green, to about 3 cm long; cones 5 to 10 cm long; Pacific coast form. (*P. taxifolia*)................................*P. menziesii*

Trees generally smaller; leaves bluish-green, averaging shorter; cones smaller, mostly to about 5 or 6 cm long; Rocky Mountains and southwest............var. *glauca*

OCCURRENCE.—*Pseudotsuga menziesii* (*P. taxifolia*): (O, MR, *C, L, Yo*); var. *glauca*: (G, Yl, GT, RM, MV, B, Z, GC).

TSUGA (Hemlock)

KEY TO THE SPECIES

Leaves flat, rounded at tip; cones oval to oblong, 1.8 to 2.5 cm long; trees to 60 or 70 m high; lower elevations in Transition and Canadian Zone forests of humid northwest. ....(Western Hemlock) *T. heterophylla*

Leaves rounded or ridged on upper surface, short-pointed at tip; cones oblong-cylindric, 2.5 to 7.5 cm long; trees 25 to 50 m high; higher elevations in Hudsonian Zone forests of Pacific slope as far south as middle Sierra Nevada....................... (Mountain Hemlock) *T. mertensiana*

OCCURRENCE.—*Tsuga heterophylla*: (O, MR, C, G); *mertensiana*: (O, MR, C, L, Yo, K).

TAXACEAE—Yew Family

TORREYA

OCCURRENCE.—*Torreya californica* (California Nutmeg): (L, Yo, S).

TAXUS (Yew)

OCCURRENCE.—*Taxus brevifolia* (Pacific Yew): (O, MR, C, G).

TAXODIACEAE—Taxodium Family

SEQUOIA (Redwood)

OCCURRENCE.—*Sequoia gigantea* (Big Tree, Giant Sequoia):[7] (Yo, K, S).

[7] *Sequoiadendron giganteum*, Bucholz, J. T., The Generic Segregation of the Sequoias. Amer. J. Bot. 26:535. 1939.

CUPRESSACEAE—Cypress Family

JUNIPERUS (Junipers and Cedars)

KEY TO THE SPECIES

Low shrubs rarely more than 1 m high.
  Leaves awl-shaped, spreading from the stems, 0.5 to 1.5 (2) cm long; more or less upright shrub with spreading (or reclining) branches, not trailing; widespread in the western parks. ....(Dwarf or Mountain Juniper, Ground Cedar) *J. communis var. saxatilis*
  Leaves short and scale-like, closely appressed to the stems; low shrub with prostrate stems creeping over the ground; northern Rocky Mountains. .... (Creeping Cedar) *J. horizontalis*
Small, often scrubby-looking trees, found generally on open or dry rocky slopes or desert plateaus.
  Trees at about 8 (or 20) m high with gray-green foliage; Sierra Nevada parks at higher elevations, on dry rocky slopes of the Canadian Zone. .... (Western Juniper) *J. occidentalis*
  Trees found at middle or lower elevations in Rocky Mountains and southwest.
    Foliage generally dark-green, relatively fine; branchlets somewhat flattened and flexuous; trees to 7 (or 15) m high; widespread, mainly in the Transition Zone. .... (Rocky Mountain Juniper) *J. scopulorum*
    Foliage light yellowish-green, rather coarse; branchlets cylindric and rather stiff; small trees rarely more than 4 to 4.5 m high; characteristic as a component of the piñon-juniper forests on the desert tablelands of the southwest (*J. utahensis*). .... (Utah Juniper) *J. osteosperma*

OCCURRENCE.—*Juniperus communis* var. *saxatilis*: (MK, O, MR, L, Yo, G, Yl, GT, RM, MV, B, Z, GC); *horizontalis*: (G); *occidentalis*: (Yo, K, S); *osteosperma* (*J. utahensis*): (MV, B, Z, GC); *scopulorum*: (G, Yl, RM, MV, B, Z, GC).

CHAMAECYPARIS

OCCURRENCE.—*Chamaecyparis nootkatensis* (Alaska Cedar): (O, MR).

THUJA

OCCURRENCE.—*Thuja plicata* (Western Red Cedar): (O, MR, G).

LIBOCEDRUS[8]

OCCURRENCE.—*Libocedrus decurrens* (Incense Cedar): (C, L, Yo, K, S).

GNETACEAE—Joint-fir Family

EPHEDRA

KEY TO THE SPECIES

Leaves (scales) and branches in opposite pairs; bracts of cones stiffish, opaque, more or less joined at base.
  Branches rather stiff, numerous, tending to form dense, more or less erect, broom-like clusters; foliage yellow-green; bases of leaves brown, persistent;

[8] The generic name, *Heyderia*, has been proposed for the 3 northern hemisphere species of *Libocedrus*, which are considered to be more closely related to our *Thuja* than to the southern hemisphere species of *Libocedrus* to which this name was first applied. Hui-Lin Li, J. Arn. Arb. 34:17-36. 1953.

not or scarcely stalked; a common species. ....*E. viridis*

Branches fewer, more lax and spreading; foliage mostly darker green; cones mostly stalked.

Leaves more or less joined at base, blunt-pointed, the bases gray, falling away from stems; openly branched shrubs, but not very lax and tending to be prostrate.

Branches smooth, bluish-green; cones 6 to 7 mm long, on stalks 5 to 15 mm long; seeds in pairs, not beaked. .... *E. nevadensis*

Branches smooth or roughish, yellow-green; cones 8 to 9 mm long, not stalked or very short-stalked; seeds usually solitary, beaked at tip. (*E. fasciculata*). ....var. *aspera*

Leaves becoming distinct at base, bristle-tipped when young, tending to be persistent; seeds 5 to 6 mm long; not common in western parks. .... *E. antisyphilitica*

Leaves (scales) and branches in 3's, more or less persistent, sheathing; cones not stalked, composed of very thin, somewhat transparent nearly distinct bracts; seeds 5 to 6 mm long, solitary or in 3's; not common in the western parks... *E. torreyana*

OCCURRENCE.—*Ephreda antisyphilitica*: (MV); *nevadensis*: (Z, GC); var. *aspera*: (GC); *torreyana*: (Z, GC); *viridis*: (MV, Z, GC).

Classification and Phylogeny of Nymphaeaceae and Allied Families

Hui-Lin Li
University of Pennsylvania, Philadelphia

The Nymphaeaceae, *sensu lato*, are a heterogeneous assemblage of plants grouped together mainly because of their aquatic habitat. The family as generally accepted is of less uniform nature than most families of flowering plants and the component genera exhibit widely varied characters in all essential features. The only characters common to nearly all genera are the presence of lactiferous vessels, air spaces and scattered vascular bundles devoid of cambium and vessels. In some genera there are idioblasts or supporting cells which frequently occur in the angles of the large intercellular spaces, especially of the petioles (De Bruyne, 1922). These characters are apparently all results of the specialized aquatic habitat and do not reflect genetic affinities. Some of these characters occur in other aquatic plants of very remote phylogenetic relationships.

The Nymphaeaceae are one of the few families of wholly aquatic plants in the angiosperms. Aquatic plants in the angiosperms are generally admitted as derivatives which have actually originated independently from many widely separated terrestrial stocks. As a rule these aquatics represent a final and specialized evolutionary stage and consequently the families are usually very small containing but few genera and species, or when large, highly specialized and homogeneous, the Nymphaeaceae, *sensu lato*, being the only exceptions.

There are eight entirely aquatic families of angiosperms. Closely associated with Nymphaeaceae are Ceratophyllaceae, with one genus and three species of nearly cosmopolitan distribution. The Podostemonaceae are the largest family with about 30 genera and 130 species. These plants form a homogeneous group of highly modified thalloid plants adapted to the rapid running water and all species are of very local occurrences. Hydrostachyaceae with one genus and about 15 species, and Tristichaceae with three genera and six species are also highly modified commonly thalloid plants related to the Podostemonaceae. Trapaceae (Hydrocaryaceae) with one genus and several species are widely distributed in the Old World. The remaining two families are the cosmopolitan monotypic Callitrichaceae and Hippuridaceae. None of these aquatic families is comparable with Nymphaeaceae, *sensu lato*, in diversity of fundamental structures among the component members.

NYMPHAEACEAE, sensu lato

As noted above, in Nymphaeaceae, in all important characters of the vegetative as well as reproductive structures, the range of variation among the genera is so great and diversified, that a similar condition is not found in any other family of flowering plants. Although all genera are aquatic plants, they vary from those with short erect sympodial rhizomes to those with short or long, unbranched or branched, horizontal rhizomes which may be

slender or fleshy and differentiated into clearcut nodes or not. Some have upright floating stems while most others are acaulescent. The flowers are all regular but vary from hypogynous to perigynous or epigynous, and cyclic, hemicyclic or spiral in the arrangement of parts. Perianth-parts are 3- or 4-, or 5-merous, definite or indefinite in number, with or without differentiation into calyx or corolla. The parts are distinct or free or in a few cases united. Anthers are either sessile or filamentous, apiculate or entire. Carpels vary from three to indefinite, free or partially or completely united, and superior, half-inferior, or inferior, in the latter case, either enclosed in various forms of the receptacle or in the perianth-tube. There are from one to few or many orthotropous or anatropous ovules attached to the inner walls of the ovary. Different types of fruits, such as nuts, pods, or berries are represented. The seeds are arillate or naked, either smooth or achinate, and with or without endosperm.

Such wide discrepancies in all fundamental structures transcend the usual concept of a family and clearly indicate the heterogeneous nature of the whole group. The genera or groups of genera are apparently not only polyphyletic but are derived from widely different stocks of little or no relationships. The family as generally accepted, is assembled on ecological and not morphological grounds, and as such, it does not fit into a phylogenetic system of classification.

Nymphaeaceae, *sensu lato,* are generally associated with Ranales, *sensu lato vel stricto.* Gundersen (1950) includes it in the Magnoliales, which are otherwise exclusively woody, instead of the Ranales, without giving any reason. The generally numerous and free floral parts indicate their relatively primitive position. Some of the genera show marked resemblance and relationship to such families as the Ranunculaceae while others indicate alliances with Papaveraceae. The scattered vascular bundles and the absence of cambium are characters similar to Monocotyledons. Also in these genera, the root hairs arise from specialized cells, a feature common among Monocotyledons but rare among Dicotyledons (Metcalfe & Chalk, 1950). In *Nelumbo,* there is indication that the two cotyledons originated as one (Lyon, 1901). All these points show the great phylogenetic significance attached to members of this group. As a result a voluminous amount of literature concerning the anatomy, morphology, and phylogeny was accumulated in the past. Various ways of interpretating the phylogenetic affinities of these plants are given by many authors (DeCandolle, 1821; Gray, 1837; Van Tieghem, 1886; Lyon, 1901; Arber, 1920).

The family is generally divided into three subfamilies, Nelumbonoideae, Cabomboideae, and Nymphaeoideae, such as recognized in Caspary's treatment (Caspary, 1888). Many authors recognize these as three separate families, for instance Small (1933), who placed all in the Ranales, and Bessey (1915), who placed Cabombaceae and Nelumbonaceae in Ranales but removed Nymphaeaceae to Rhoeadales. Hutchinson (1926) accepted Cabombaceae, but retained *Nelumbo* in Nymphaeaceae. In the following treatment, the whole assemblage is divided into five groups, each accorded with the rank of a family.

NELUMBONACEAE

The genus *Nelumbo,* representing solely the subfamily Nelumbonoideae

(Caspary, 1888), has been early made into the family Nelumbonaceae by Lindley (1836). It has long been recognized as a very isolated group of plants, generally as a tribe or subfamily in Nymphaeaceae. There are two species in the genus, one in the warmer parts of Asia to northeastern Australia and another (sometimes as two species) of Atlantic North America southward to Colombia. These species are in many ways unique and very different from the other genera of Nymphaeaceae, *sensu lato*. The large fleshy rhizomes are branched and marked distinctly with nodes and internodes, a type resembling strongly some Monocotyledons. The long stalked peltate leaves at once assume their adult form, while the other genera with peltate leaves bear first an awl-shaped leaf followed by lanceolate, sagittate or ovate submerged leaves before the development of the adult floating form. The perianth-parts are very numerous and free and together with the numerous free stamens, are spirally arranged. Above the stamens there is the unique large obconical spongy receptacle with numerous carpels each buried in a round pit in the flat upper surface. Each carpel contains a pendulous anatropous ovule on the side toward the axis. The carpels ripens into an indehiscent nut with very hard pericarp and completely filled by the embryo with no endosperm. The embryo consists of two large fleshy hemispherical cotyledons and a green plumule enclosed by a thin membranaceous sheath sometimes interpretated as endospermous (Lyon, 1901). The two cotyledons originated around the base of the plumule in the form of a ring which later becomes two-lobed, a condition suggesting that actually there is only one cotyledon (Lyon, 1901).

All these features make *Nelumbo* a most unique and distinct genus. It suggests relationships with certain Monocotyledonous plants in the vegetative structures and in the cotyledons. Lyon (1901) even considers that *Nelumbo* conforms to the type of Monocotyledons in both anatomy and embryogeny and suggests Nymphaeaceae as a whole should be classified in Monocotyledons as a subseries in Helobiae. The many vascular bundles in the rhizome are arranged in several concentric circles, the innermost are held by Van Tieghem (1866) to constitute a central cylinder surrounded by a common endodermis.

To a certain extent, the genus *Nelumbo* also suggests relationships with herbaceous genera of Berberidaceae. It shows stronger affinities with Magnoliales than other genera of Nymphaeaceae, *sensu lato*, especially in the numerous spiral floral parts. The receptacle with immersed carpels closely resembles that of *Eupomatia*, a shrub of New Guinea and Australia and the monotype of Eupomatiaceae of Magnoliales.

Many recent floristic works recognize the familial status of Nelumbonaceae. Because of the distinct isolated nature, the genus *Nelumbo* should not only be segregated as the type of a distinct family but also that of an order Nelumbonales, to be placed between Magnoliales and Ranales. It is a primitive group derived early from ancestral Angiosperms that give rise to different groups of Dicotyledons as well as Monocotyledons. Because of its many unique features, *Nelumbo* occupies a relatively isolated position in phylogeny.

CABOMBACEAE

The subfamily Cabomboideae in Caspary's system (1888) consists of two genera *Cabomba* and *Brasenia* and has been recognized by Gray (1839) and followed by Bessey (1915), Hutchinson (1926) and others as representing

a distinct family Cabombaceae, with good reasons. *Cabomba* contains six species in the warmer parts of America. *Brasenia* is monotypic and cosmopolitan outside Europe.

These two genera are distinct from all others in possessing long slender floating stems in addition to erect sympodial rhizomes. The stem is coated with a mucilagenous secretion and bears spirally arranged floating peltate leaves, and in *Cabomba*, also decussate deeply cut submerged leaves. The flowers are small, axillary and lateral, with distinct hypogynous cyclic parts. There are three sepals and three petals, followed by 3-6 (*Cabomba*) or ∞ (*Brasenia*) stamens and 3 (*Cabomba*) or ∞ (*Brasenia*) free carpels. The ovules are few and borne on the sides of the carpels. The fruits are indehiscent pods with generally three pendulous seeds. The embryo is surrounded by a small layer of endosperm and there is copious perisperm.

In the internal anatomy as with the flower structure, these two genera, with only two pairs of vascular bundles, show great simplicity as compared with other genera of the Nymphaeaceae, *sensu lato* (Gwynne-Vaughan, 1897).

The recognition of Cabombaceae as a family is now generally accepted. Cabombaceae are clearly related to Ranunculaceae as revealed by the general habit, the small flowers with free, hypogynous parts and the fruits. The dimorphic leaves of *Cabomba* strongly recall the *Batrachium* section of *Ranunculus*. Cabombaceae are therefore to be placed definitely in Ranales. As a family it represents a modified type deriving from certain families like the Ranunculaceae and adapting exclusively the aquatic habitat. Further specialization and adaptation in this direction apparently lead to the development of the family Ceratophyllaceae (Gray, 1837).

EURYALACEAE

There are four tribes in the subfamily Nymphaeoideae of Caspary (1888), who follows the earlier scheme of Endlicher (1839), namely, Euryaleae, Eunymphaeae, Nuphareae, and Barclayeae. This whole group is the same as Nymphaeaceae, *sensu lato*, of many recent authors. These genera are all characterized by the union of carpels in different degrees into a single many-celled ovary bearing more or less radiating stigmas. Because of this, Bessey (1915) placed Nymphaeaceae in Rhoeadales. However, it seems that these generalized characters are in no sense distinct as they occur also in many other families. Again, as discussed below, this is a very heterogeneous assemblage and these tribes indicate different affinities.

Among these tribes, Euryaleae consist of two genera, *Euryale*, and *Victoria*. *Euryale* is a montotypic genus of eastern Asia. *Victoria* has two or three species along the Amazon region in South America. These plants are distinguished by the huge peltate floating leaves and completely epigynous 4-merous flowers. The rhizome is short, thick and erect, which lives for one year in *Euryale* and for a few years in *Victoria*, while in other genera of Nymphaeaceae, *sensu lato*, the rhizomes are mostly long-lived. The surfaces of the different organs are covered with strong prickles. These characters, together with lactiferous ducts, radiating stigmas and abundant ovules attached to the wall of the ovary, which are common characters of other genera as well, indicate strong affinities with Papaveraceae. These two genera are also characterized in having the pollen grains shed in tetrads.

Euryale and *Victoria* are thus remote from the other genera, with possibly the exception of *Barclaya* as will be noted below, and should be made into a family of their own to be placed probably in or near Rhoeadales instead of Ranales. As a family it can be considered as a derived and modified type related to Papaveraceae that develops an inferior ovary. Many other aquatic plants with inferior ovary, such as *Trapa, Trapella, Hippuris,* and the aquatic genera of Haloragaceae, can be similarly traced in their relationships with terrestrial plants with superior ovary. The inferior position of the ovary apparently gives added protection against aquatic animals.

NYMPHAEACEAE, sensu stricto

The tribe Eunympheae of Endlicher (1839) and Caspary (1888) comprises the genera *Nymphaea* and *Castalia* with the latter sometimes included in the former. There are about 50 species widely distributed in warm and temperate parts of the World. There is either a long-lived stout and short erect rhizome (*Castalia*) or a long- or short-lived creeping and branching one (*Nymphaea*). There are four sepals followed by numerous spirally arranged large petals passing gradually into numerous stamens. These are perigynous and the ovary is half-inferior. The carpels, varying from 5-35, sunk in the receptacle, partly fusing below and extending into a stylar process above. There are numerous ovules inserted on the inner wall of the ovary. The carpels vary in degree in their lateral union, indicating an apocarpous ancestry. The fruit is a spongy berry dehiscing regularly by the swelling of the mucilage which surrounds the numerous seeds. The seed is enclosed within a fleshy aril with a small embryo, scanty endosperm and copious perisperm.

Closely related to *Nymphaea* is *Nuphar,* the monotype of the tribe Nuphareae of Endlicher (1839) and Caspary (1888). There are about seven species distributed in the north temperate regions. The genus resembles *Nymphaea* in the stout creeping rhizome, in the leaves with a sinus at base, and in the numerous spiral petals and stamens. The sepals are five instead of four and the petals are small, scale-like, bearing a nectary on the back. The pistil is also syncarpous, but superior, formed of ten to sixteen carpels with ray-like stigmas. The ovules are also numerous and attached to the walls of the ovary. The fruit also dehisces with the swelling of mucilage. The structure of the seed resembles that of *Nymphaea* but is without an aril.

As here interpreted, *Nymphaea, Castalia,* and *Nuphar* constitute the family Nymphaeaceae, *sensu stricto.* As originally formulated by DeCandolle (1821, 1824), the family Nymphaeaceae consists of the genera *Nymphaea* (including *Castalia*), *Euryale,* and *Nelumbo.* The genera *Cabomba* and *Brasenia* were included by him in Podophyllaceae. Nymphaeaceae, *sensu stricto,* are here circumscribed to include only *Nymphaea, Castalia,* and *Nuphar.*

The position of Nymphaeaceae is in the Ranales. The scattered vascular bundles, a character shared by other genera as well, suggest affinities with the herbaceous Berberidaceae (Podophyllaceae) as is also the arillate seed of *Nymphaea.* The family should be placed near Ranunculaceae and Berberidaceae.

BARCLAYACEAE

The tribe Barclayeae of Endlicher (1839) and Caspary (1888) with one genus *Barclaya* is very distinct from the other genera of Nymphaeaceae, *sensu lato,* with which it is associated by the original author Wallich (1827). There are about four species in the tropics of Asia. There is a short or long, villose rhizome. The leaves are linear-oblong and hastate or oblong-orbicular and cordate. This type of leaves is the most primitive as compared with the other genera (Gwynne-Vaughan, 1897). The flower is most unique in having five sepal-like bracts below the ovary, and a tubular perianth enclosing the ovary in its lower part, which may be called the torus, and with numerous epipetalous stamens on the upper inner surface. The upper part of the perianth is many-lobed with the lobes in several series. There are about ten confluent carpels prolonged into a conniving style forming a ten-rayed cone, stigmatiferous within. There are many orthotropous ovules scattered parietally. The fruit is a globose berry crown by the perianth-tube. The seeds are characteristically echinate, with floury endosperm and a minute embryo.

The bracts were originally described as sepals and are still considered by some authors as such, but Hooker (1852) is apparently right in interpreting these as an involucre. The very distinct flower, as noted by Hooker (1852), bears some resemblance to that of *Eurydale.* In the flower of *Barclaya,* however, the union of the perianth-parts is carried further. The genus apparently represents a further stage of specialization. *Barclaya* is still little known and has not been examined in detail morphologically.

There is little in its character to suggest close affinities with Ranales. The united perianth in particular precludes the possibility of including it in the later. In the whorled perianth-parts and the numerous parietal ovules, the genus rather indicates relationship with Papaveraceae. The general floral structure shows closeness to *Euryale* but these two genera differ from each other in many important characters. Thus *Barclaya* is an isolated genus best considered as representing the type of a distinct family Barclayaceae.

Barclayaceae and Euryaleaceae could probably be included in Rhoeadales provided that the scope of the order be modified and enlarged for their accommodation. These aquatic genera represent a more advanced stage of development than their nearest terrestrial relatives. In the united perianth and the inferior ovary, some relationship of these aquatic genera to the Aristolochiaceae is indicated. A more desirable alternative is to establish a separate order Euryalales for these two families of aquatic plants, to be placed after Rhoeadales and Aristolochiales, indicating a more advanced stage of development.

TAXONOMIC DESCRIPTIONS

A systematic account giving descriptions of the families concerned, originally all included in the Nymphaeaceae, *sensu lato,* is as follows.

RANALES

CABOMBACEAE A. Gray in Ann. Lyceum Nat. Hist. New York. 4:46. 1837.

Aquatic perennial caulescent herbs, with slender rhizome. Stems long, leafy, coated with mucilage. Leaves floating and immersed, palmately veined, either all peltate, undi-

vided or alternate, or the floating alternate and the submerged palmately dissected and opposite or whorled.

Flowers small, single on long axillary peduncles, all parts hypogynous and free. Sepals and petals 2 each or sometimes 4 each, persistent, the petals white, yellow or purple. Stamens definite in number, 3-18; filaments slender; anthers usually extrorse; connectives continuous with the filaments. Carpels 2-18, distinct; stigmas terminal, linear, sessile or nearly so; ovules 2 or 3, orthotropous, pendulous on the sides of the ovary wall or the dorsal suture, or when 3, one of the them near the ventral suture. Fruits of several coriaceous free and distinct indehiscent nut-like carpels. Seeds 1-3, often 2. Embryo at the base of the fleshy endosperm; cotyledons fleshy; hypocotyl very short.

Two genera, *Cabomba* with six species in the warmer parts of North America, and *Brasenia,* one species, North America, Asia, Africa, and Australia.

NYMPHAEACEAE DC. Prop. Med. Ed. 2, 119. 1816, Prodr. 1:113. 1824, pro parte.

Perennial aquatic acaulescent herbs, with cylindrical thick horizontal rhizome. Leaves long-petiolate, arising from the rhizome, alternate, with a distinct sinus at the base, not peltate.

Flowers solitary, axillary, on long peduncles arising from the rhizome. Sepals 4-6 or more, often green, free or nearly so. Petals numerous, large or small, in many series, usually passing into staminodes or stamens, hypogynous or perigynous, adnating variously to the ovary. Stamens ∞, inserted with the petals; anthers introrse, adnate. Ovary compound, of 3-35 united or partially united carpels; stigmas ∞, united into a disk with radiating rays; ovules very numerous, pendulous, inserted on the inner walls of the ovary. Fruit a coriaceous many-seeded berry. Seeds with endosperm, with or without an aril.

Two or 3 genera, *Nymphaea, sensu stricto,* with about 10 species in northern temperate regions, *Castalia* (sometimes as a distinct genus (Schuster, 1907) or included in *Nymphaea* (Conard, 1905)) with about 40 species, widely distributed in the northern and southern temperate and tropical zones, and *Nuphar,* about 7 species in the North Temperate Zone.

Nelumbonales, ord. nov.

Characters of the family.

NELUMBONACEAE Lindl. Nat. Syst. Ed. 2, 13. 1826 (Originally as "Nelumbiaceae").

Large aquatic perennial herbs, with large thick fleshy creeping rhizomes with distinct nodes and sessile scales. Leaves long-petiolate, floating or mostly arising high above water from the rhizome, circular, centrally peltate and depressed or cupped.

Flowers large, showy, yellow, pink, or white, the sepals, petals and stamens hypogynous; scapes arising with the petioles, stout, tall, each terminating by a single flower. Sepals 4 or 5, imbricate, passing gradually into the petals, caducous. Petals and stamens ∞, caducous; filaments long, more or less petaloid; anthers narrow, extrorse, the connective prolonged into a slender incurved appendage at top. Carpels ∞, distinct, immersed singly in pits in the large broad summit of the large turbinate spongy receptacle; ovary 1-celled; stigma umbilicate; ovules solitary or rarely 2, pendulous, anatropous. Fruits of many oblong or globose nuts, immersed in the accrescent receptacle. Seeds without endosperm. Embryo of 2 thick fleshy cotyledons in a delicate stipule-like sheath, enclosing a plumule of 2 or 3 well developed young leaves.

One genus, *Nelumbo,* with 2 species, one in Atlantic North America south to Colombia and one in the warmer and tropical parts of Asia to northeastern Australia.

Euryalales, ord. nov.

Herba natans, acaulis. Calyx tubo cum ovario adnato. Corolla gamopetala, inferne

cum tubo calycis unita, vel semi-polypeltata, petala summo calycis tubo inserta. Stamina plurima, cum petalis inserta, multiseriata. Ovarium inferum, ovulis dissepimentorum parietibus insertis.

Euryalaceae, fam. nov.

NYMPHAEACEAE subfamily Nymphaeoideae tribe Euryaleae
Endlicher, Gen. Pl. 899. 1839.

Herba natans, acaulis; pedunculis petiolis calycibus foliorumque nervis aculeatis; foliis magnis vel giganteis, natantibus, peltatis, orbiculatis, subtus valide nervosis. Scapi simplices, uniflori. Flores magnis vel pro magnitudine plantae parvis, speciossimus.

Calyx tubo campanulato vel urceolato, cum ovario connato, limbi superi, quadripartiti, lobis intus coloratis, persistentibus vel deciduis. Corolla petala indefinite plurima, summo calycis tubo multiseriatim inserta, libera, limbo breviora vel longiora, interiora minora. Stamina plurima, cum petalis inserta, multiseriata, libera, exteriora fertilia, filamentis petaloideis vel subpetaloideis, antheris introrsis, bilocularibus, loculis adnatis, longitudinaliter dehiscentibus, interiora sterilia, libera vel stigmatum dorso adnata. Ovarium infernum, subglobosum, 6-8 vel multiloculare. Ovula in loculis 6-8 vel plurima, dissepimentorum parietibus inserta, anatropa. Stigma peltatum vel campanulatum, radiatum, centro umbilicatum, liberum. Bacca ovata vel cyathiformis, 8-multiloculata, calycis limbo stigmateque coronata. Semina plurima vel abortu ovulis multo pauciora, interdum intra pulpam nidulantia, globosa vel subglobosa, testa nucamentacea. Albumen copiosum, carnosum.

Two genera, *Euryale,* 1 species in eastern Asia, and *Victoria,* 2 or 3 species along the Amazon region in South America.

Barclayaceae, fam. nov.

NYMPHAEACEAE subfamily Nyhphaeoideae tribe Barclayea
Endlicher, Gen. Pl. 899. 1839

Herba natans, acaulis, rhizomate ovoideo vel longo, villoso; foliis petiolatis, elongatis, oblongis vel rotundatis, basi paullo angustata-cordato-subhastatis vel cordatis, haud peltatis, membranaceis vel chartaceis, glabris vel subtus tomentosis. Scapi folio breviores, simplices, uniflori. Involucri persistentis vel deciduis, 5-phylli, foliola distincta oblongo-lanceolata, ad basim floris verticillata, concava, patentia, uninervia, membranacea, extus infra apicem mucronata.

Calyx 4-5-lobus, tubo elongato inferne cum ovario adnato, lobis linearibus erectis distinctibus. Corolla gamopetala, inferne cum tubo calycis unita, limbi brevis, 8-∞-lobi, lobis 2-3 seriatis, inaequalibus. Stamina plurima tubo perianthii pluriseriatim inserta, libera, inclusa, seriebus alternatis, remotis, duabus supremis sterilibus, subulatis, incurvis, reliquis fertilibus, filamentis brevissimus, subulatis, antheris basifixis, oblongis, bilocularibus, loculis longitudinaliter dehiscentibus. Ovarium inferum, oblongum vel globosum, 10-loculare, loculis pluriovulata, pulpa gelatinosa repletis matura fructus fere obsorpta, ovulis dissepimentorum parietibus insertis. Stylus conicus, brevissimus; stigmata depresso-umbilicata, obscure radiata, margine 10-15—laciniata, laciniis subulatis, erecto-conniventibus. Bacca carnosa, globosa, matura calyce mucronata. Semina plurima, globosa, testa membranaceo, setis hyalinis, succulentis, patentibus, juxta verticem obsolete umbilicatum densuis confertis echinata. Albumen carnosum. Embryo minimus.

One genus, *Barclaya,* about 4 species in tropical Asia.

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Prediction of an Introgressant in Viola

Norman H. Russell and Miwako Cooperrider
Grinnell College, Grinnell, Iowa

During the spring of 1949, while the senior author was engaged in studies upon a hybrid swarm of acaulescent white violets in the Ham Lake Meadow north of Minneapolis, Minnesota, he noticed a second hybrid swarm occurring in the northwestern and western part of the same meadow. One parent of these second hybrids was apparently *Viola sagittata* Ait., as this species was abundant over the remainder of the meadow, and the hybrids often possessed morphological characters typical of *V. sagittata.* The other original parent of the hybrids, however, was not found in the immediate vicinity, despite an intensive search.

The Ham Lake Meadow is located about ½ mile south of Ham Lake, a small lake adjacent to Minnesota Highway 65, about 35 miles north of Minneapolis. It is a boggy field of about 9 acres (fig. 1), much disturbed by grazing in the past, though apparently, never cultivated and not grazed for a number of years prior to 1949. A few trees grew along an old, filled drainage ditch to the east and in the northwestern corner of the meadow, but otherwise only herbs and low shrubs were found. The meadow is bounded on the north by a deep, water-filled drainage ditch, the south by a dirt road, and the east and west by cultivated fields on higher ground. Many bog plants attest to its former nature.

Several population samples were taken of *V. sagittata* and the hybrid in 1949 and 1950. Material of two spring and two summer collections from 1949 was chosen for the present analysis. The population samples consist of plants taken at random through the area of each entity. Whole plants, sometimes consisting of several crowns growing from branched, subterranean rhizomes, were taken, washed, pressed, and stored. To avoid obtaining members of the

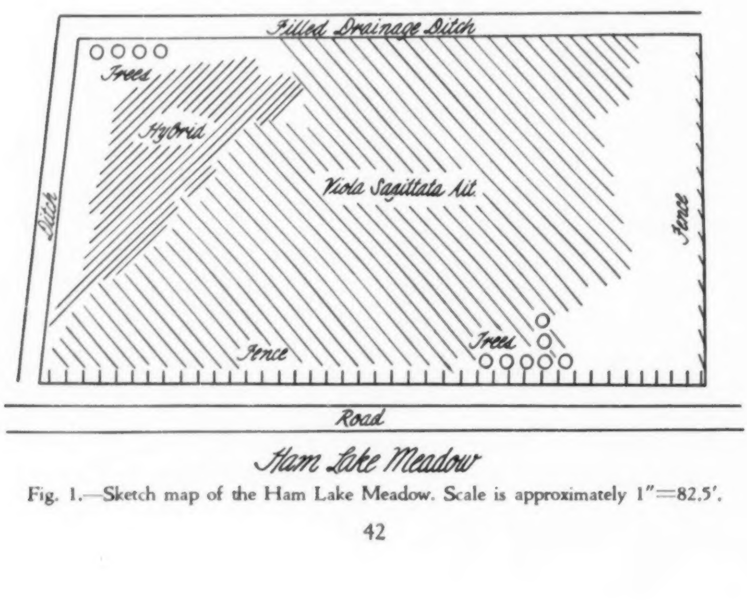

Fig. 1.—Sketch map of the Ham Lake Meadow. Scale is approximately 1″=82.5′.

Fig. 2.—Typical spring appearance of plants of *V. sagittata* (left) and of the hybrid (right). Drawn from herbarium specimens. Scale: 1:2.

same vegetative clone the plants taken were not less than ten feet apart. The different collections were made in the *areas* of the respective entities; no search was made for unusual or *typical* specimens. The areas of *V. sagittata* and the putative hybrid were rather sharply delimited. The northwest corner of the field, especially, was slightly higher and drier than the remainder of the field where *V. sagittata* flourished. Where the two entities met, *V. sagittata* was found at the bottom of small, shallow ditches, the hybrid plants along the sides. A series of 25 small quadrats was run in the field on May 19, 1949. It was found that *V. sagittata* had a frequency percent of 36 compared to 4 percent for the hybrids. One hundred forty-four crowns of *V. sagittata* and 15 crowns of the hybrids were counted in the plots.

The absence of one parent of the hybrid swarm presented a problem not unique, but certainly unusual. Anderson (1949) presented his method of "extrapolated correlates" for analysis and prediction in such events, and this seemed an excellent opportunity to use it. To our knowledge no case of its use in a situation as appropriate as the present had appeared in the literature. This method supposes that in the event of free or even partial interbreeding between two species there will be a tendency for introgression or the movement of chromosomes or chromosome fragments to take place between the two species. Therefore, in the event of the absence of an original parent, it should be possible to predict its nature by careful correlation of the morphological,

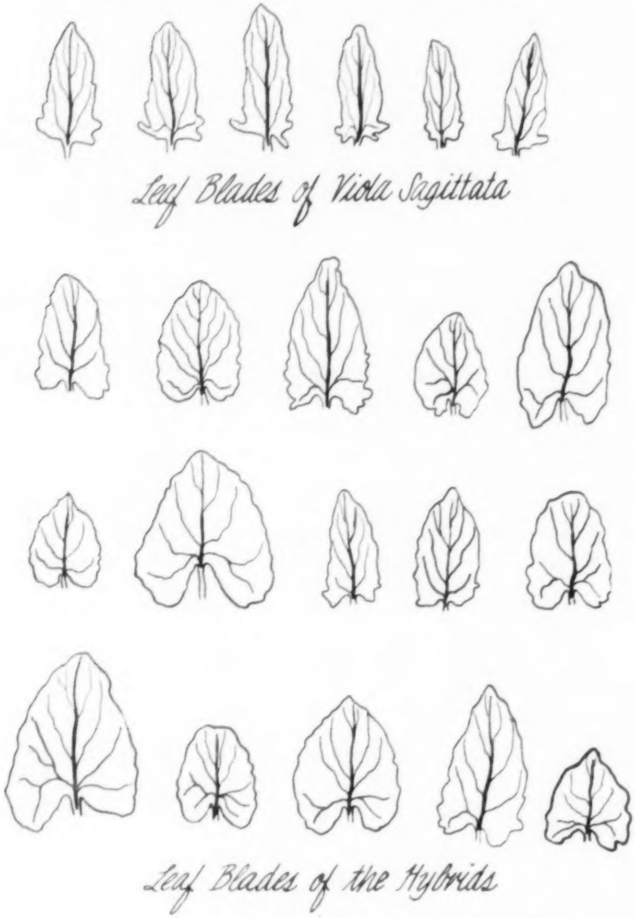

Fig. 3.—Leaf outlines of *V. sagittata* and the hybrids, traced from pressed leaves. Scale: 1:2.

physiological, or ecological characters of the hybrid and the remaining parent, and then by extrapolation from them in the direction away from the known parent. Anderson (1949) illustrated the method by using Riley's (1938) data on *Iris fulva* and *I. hexagona* var. *giganti-caerulea* and their hybrids, setting up a purely hypothetical case.

DESCRIPTIONS OF VIOLA SAGITTATA AND THE HYBRIDS

Viola sagittata is found from Massachusetts to Minnesota and south to Georgia and eastern Texas. The northwestern form, occurring westward from Indiana to Minnesota and Iowa, is a small, acaulescent blue-flowered violet. It is characterized by leaves which are narrowly ovate, hastate at the base, and

which have, when mature, about three marked basal teeth or short lobes on each side of the lamina. The leaves are usually densely pubescent on both upper and lower surfaces of the blades, and in addition the petiole may be villous along its whole length or, more often, only in its distal portion. This is in marked contrast to the glabrous plants of the eastern states. The petals of the open flowers are purple with white bases. Cleistogamous flowers are sagittate, having long-clawed sepals.

The hybrid plants presented a motley aspect. Most were larger than adjacent *V. sagittata* plants, especially in the spring. They produced, in addition, more crowns per rootstock, more open flowers in spring, and more cleistogenes in the summer. The hybrids varied most noticeably in leaf shape, some having ovate, toothed leaves as in *V. sagittata*, others having reniform, unlobed leaves. In fig. 2 typical plants of *V. sagittata* and the hybrid are illustrated, and in fig. 3 a number of leaves of each has been drawn illustrating variation in leaf shape. As might be expected, variation was much greater in the hybrids.

METHODS

The four population samples were analyzed separately. Twenty-five plants were measured of each of the samples except HLM-48, where only 18 plants were pressed sufficiently well for measurement, and NR 519494, with 24 plants. On each plant of the two spring collections (NR 519494-*V. sagittata* and NR 519495-hybrid) the following characters were observed, measured, or computed:

Length of spur petal
Breadth of spur petal
Spur petal length:breadth ratio
Length of sepal
Length of sepal claw
Sepal length:claw length ratio
Length of peduncle
Distance from base of peduncle to first bracteole
Peduncle length:distance to bracteole ratio
Lamina length (shortest)
Lamina breadth (greatest)
Lamina length:breadth ratio
Basal angle of lamina (angle of divergence of the basal lobes from a line at right angles to the petiole and midrib. The value given was positive for cordate leaf bases, negative for cuneate bases.)
Petiole length
Petiole pubescence (according to the scale: 0-glabrous; 1-pubescent in upper third only; 2-slightly pubescent over whole length; 3-very pubescent over whole length.)

On the two summer collections (NR 812494-hybrid, and HLM-48-*V. sagittata*) the following characters were observed, measured, or computed:

Cleistogene sepal length
Cleistogene sepal claw length
Sepal length:claw length ratio
Cleistogene peduncle length
Distance from base of peduncle to first bracteole
Peduncle length:distance to bracteole ratio
Peduncle position (according to the scale: 0-erect; 1-ascending at angle of about 45° from ground; and 2-prostrate.)
Lamina length (shortest)
Lamina breadth (greatest)
Petiole length
Basal angle of lamina (see above)
Number of teeth (lobes) on one side of lamina
Pubescence upper surface of lamina (4 grades: 0-glabrous; 1-pubescent on major veins only; 2-sparsely pubescent over lamina surface; 3-densely pubescent over whole surface.)
Pubescence of lower surface of lamina (scale as above)
Petiole pubescence (same scale as for spring collections)
Lamina length:breadth ratio

These particular characters were chosen after a close examination of the material. They were characters which seemed to be correlated and to differ

between the two entities on visual inspection.

Pictorialized scatter diagrams (Anderson, 1949) were prepared for each of the four collections. Those for the two spring collections are figs. 4 and 5 and for the summer collections figs. 6 and 7. A total of 9 characters were used in figs. 4 and 5 and 7 characters in figs. 6 and 7.

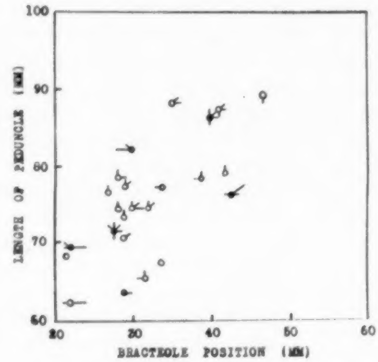

Fig. 4.—Pictorialized scatter diagram for the 24 plants of the spring collection of *V. sagittata* (NR 519494). See text for key to symbols.

These figures were prepared as follows: First the variation of each character used was plotted. Next values of 0, 1, and 2 were assigned, the value 0 to that end of the scale representative of *V. sagittata*, of 2 to the other end of the scale, and of 1 to intermediate values. An example is the assignment of values to sepal:sepal spur ratio of open flowers in the spring collection, as below:

LENGTH OF SEPAL:LENGTH OF SEPAL SPUR RATIO

Ratio	Number of Plants: *V. sagittata*	Number of Plants: Hybrid	Value
3.00-3.25		2	
3.26-3.50			
3.51-3.75			
3.76-4.00	1	1	
4.01-4.25			2
4.26-4.50		2	
4.51-4.75	1	2	
4.76-5.00	1	10	
5.01-5.25			
5.26-5.50			
5.51-5.75	1	1	1
5.76-6.00	6	4	
6.01-6.25			
6.26-6.50	1		
6.51-6.75	1	1	
6.76-7.00	9	1	
7.01-7.25		1	0
7.26-7.50	1		
7.51-7.75			
7.76-8.00	1		
8.01-8.25			
8.26-8.50			
8.51-8.75			
8.76-9.00			
9.01-9.25			
9.26-9.50	1		

The assignment of values for each character was, of course, somewhat arbitrary, but great accuracy is not required by this method.

On the charts the values are represented by symbols. On both charts length of peduncle from base to first bracteole is plotted on the abscissa, and total peduncle length on the ordinate. In figs. 4 and 5, the two spring collections, the values were represented by the following symbols:

Length of Spur Petal

Range	Value	Symbol
13-15	0	0
16	1	0
17-20	2	0

Sepal:Sepal Spur Ratio

Range	Value	Symbol
9.5-6.1	0	0
6.0-5.1	1	0–
5.0-3.0	2	0—

Length of Petiole

Range	Value	Symbol
10-40	0	0
41-70	1	0
71-140	2	0

Blade Length:Breadth Ratio

Range	Value	Symbol
3.75-2.10	0	0
2.00-1.51	1	–0
1.50-0.75	2	—0

Basal Angle of Lamina

Range	Value	Symbol
—20° to +20°	0	0
+21° to +45°	1	\0
+46° to +80°	2	\0

Pubescence on Petiole

Range	Value	Symbol
0	0	0
1-2	1	0/
3	2	0/

Length of Sepal

Range	Value	Symbol
4.5-6.5	2	●
6.6-9.0	0	0

In figs. 6 and 7, representing the summer collections, the values and symbols were as follows:

Peduncle Position

Range	Value	Symbol
Erect	0	0
Ascending	1	0
Prostrate	2	0

Sepal:Sepal Spur Ratio

Range	Value	Symbol
3.00 or less	0	0
3.01-3.50	1	C–
3.50 or more	2	0—

Basal Angle of Lamina

Range	Value	Symbol
+25° or less	0	0
26° to 40°	1	0
41° or more	2	0

Lamina Teeth on One Side

Range	Value	Symbol
3 or 4	1	–0
1 or 2	0	–0
0	2	—0

Blade Length:Breadth Ratio

Range	Value	Symbol
1.01 or above	0	0
1.00 or below	2	●

There is a general correlation among the characters used in all four graphs, indicating that introgression has occurred. Data from the scatter diagrams and other measurements point toward a plant with the following characters as being the unknown parent of the hybrid swarm.

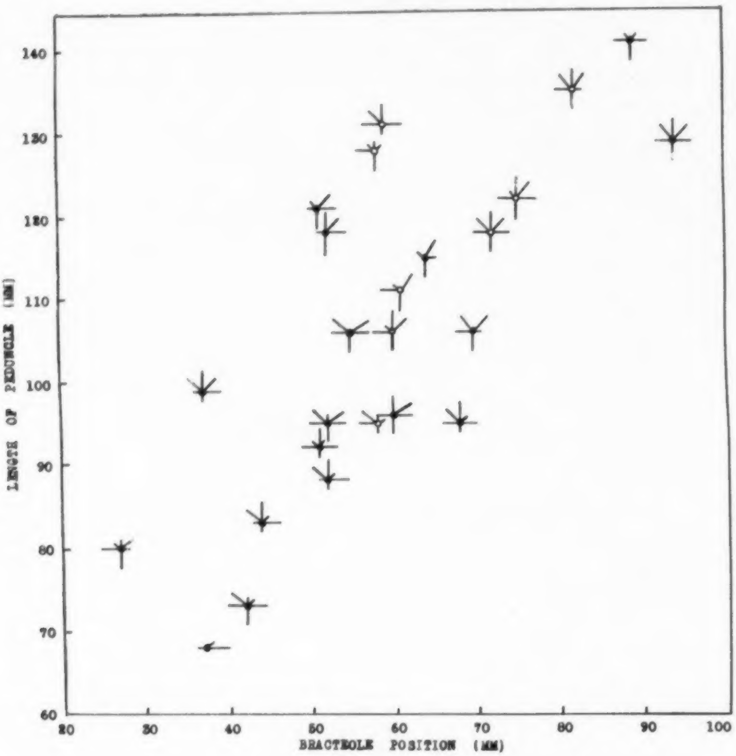

Fig. 5.—Pictorialized scatter diagram for the 25 plants of the spring collection of the hybrids (NR 510495).

Lamina length:breadth ratio of about .75 for young leaves and of about .60 for later leaves indicating the leaves to be broad-cordate to reniform in shape; Bracteoles about midway along the peduncle; Cleistogamous peduncle position prostrate; Cleistogamous peduncles relatively short; Basal angle of mature lamina of about 30°, indicating relatively shallow basal lobes; Sepal:sepal claw ratio of 3.50 or more, indicating relatively shallow basal lobes; Lamina margin not toothed, but crenate; Petiole pubescent; Lamina pubescent on both surfaces; Plants relatively large.

CONCLUSIONS

In the flora about Minnesota there are four violets which belong to the same Section (*Boreali-Americanae*) of the genus *Viola* as *V. sagittata* and which are rather frequently found. These are *V. pedatifida*, *V. nephrophylla*, *V. papilionacea* and *V. sororia*. In addition there are four other species which are only rarely found within 100 miles of the Twin Cities: *V. cucullata*, *V. missouriensis*, *V. septentrionalis*, and *V. affinis*. All of these violets except *V. sororia* may be eliminated from consideration as the unknown parent of the hybrids on the basis of at least one and usually several of the predicted char-

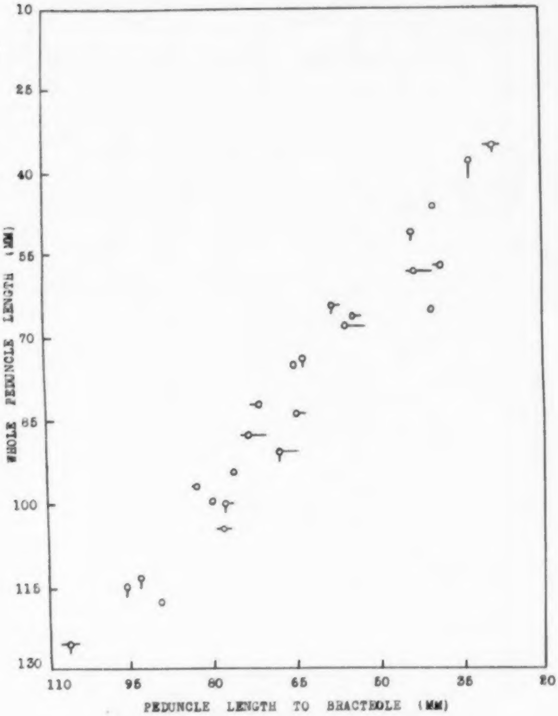

Fig. 6.—Pictorialized scatter diagram for the 25 plants of the autumn collection of *V. sagittata* (HLM-48).

acters listed above. For example, *V. nephrophylla, V. papilionacea, V. cucullata,* and *V. affinis* are typically completely glabrous. *V. pedatifida* has deeply dissected leaves. *V. nephrophylla* and *V. cucullata* have erect cleistogenes. *V. missouriensis* has attenuate, usually glabrous leaves. *V septentrionalis* has ciliolate sepals. *Viola sororia,* at least in the Minneapolis region, satisfies every requirement. After the above list was prepared, the following description of *V. sororia* was excerpted from Fernald (1950) and Brainerd (1921).

Leaves cordate-ovate
Petioles densely villous
Lower laminas densely villous
Mature leaves dark green
Mature leaves thickish
Larger mature leaves 6-13 cm. broad
Larger mature leaves with 21-52 prominent teeth on each margin
Petaliferous flowers about equaling to overtopping leaves
Petaliferous flowers violet or lavender
Spurred petal glabrous or only sparsely hairy
Outer sepals ovate-oblong
Sepals obtuse
Sepals more or less ciliate toward base
Sepal auricles short and broad appressed
Cleistogenes on fleshy peduncles
Cleistogamous peduncles buried but later arching
Capsules usually purplish
Capsules ovoid
Seeds buff to brown
Seeds plump-ovoid
Seeds 1.75-2.5 mm. long
Seeds 1.2-1.5 mm. thick

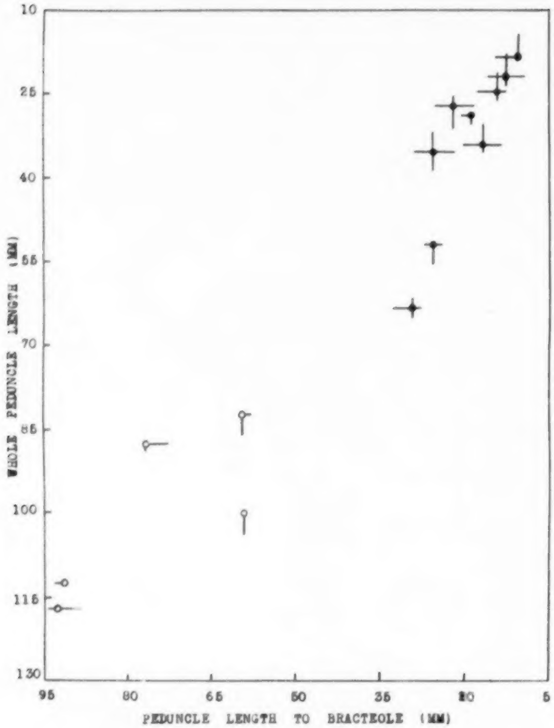

Fig. 7.—Pictorialized scatter diagram for the 14 plants of the autumn collection of the hybrids (NR 812494).

The pictorialized scatter diagrams then point unmistakably to *Viola sororia* Willd. as the other original parent of the hybrid swarm.

Viola sororia has been found by the senior author growing sparsely in a woodland about ½ mile east of the Ham Lake Meadow. Whether these plants are the parents of the hybrids here studied, or whether a closer group of plants, eliminated in the past by cutting of forests in or adjacent to the meadow, were the parents, is difficult to ascertain. The presence of a few small trees in the northwestern corner of the meadow may be an indication of the presence of woodland here in the past. This area was very probably tree-covered when the first white men came, as old oak forests surround the cultivated fields here. A long absence of one, or even both, original parents, would not necessarily spell the doom of the hybrids. These violets are perennials and are capable of indefinite vegetative propagation by rhizome growth and fragmentation, even though few or no viable seeds are produced. Brainerd (1904) ventured the suggestion that new "species" or forms might be established by apomictic reproduction of sterile hybrids or hybrid segregates.

Introgression into *V. sagittata* is here clearly indicated by the presence of numerous plants which, though generally within the range of characters of *V.*

sagittata and growing in the wetter parts of the meadow, have certain of the characters of *V. sororia*. By reference to fig. 4, it will be seen that every character but petiole length has introgressed to some extent. In the fall material (fig. 6) all characters but peduncle position have apparently introgressed slightly into *V. sagittata*.

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A Histological Study of Regeneration in the Epicotyl of Tomato

Alfred T. Collette and Norman J. Gillette
Syracuse University, Syracuse, New York

Investigations on regeneration in plants may be divided into categories including those involving the application of growth substances and those which do not involve the application of growth substances.

During recent years, a vast amount of research has been conducted to demonstrate the effects of various growth substances on plants. Of particular significance are the investigations of Kraus et al. (1936) who studied the responses of bean plants to indoleacetic acid and Borthwick et al. (1937) who carried out an investigation to determine the reaction of tomato plants to indoleacetic acid. The results of investigations in this category show a wide variety of patterns and have been adequately reviewed by Avery and Johnson (1947), Mitchell and Marth (1947), and Skoog (1947, 1951).

Investigations on regeneration not involving the application of growth substances have been reviewed by Swingle (1940, 1951), Guillermond (1942) and White (1936, 1946). Of particular interest in this category are the works by Crooks (1933) whose study dealt with regeneration in flax seedlings and Bain (1940) who determined the origin of adventitious shoots in decapitated cranberry seedlings.

It was noted by Wildman (1952) that when tomato seedlings were decapitated and treated with lanolin, a callus resulted on which buds and leaf primordia were frequently observed. The present investigation is a histological study of the changes which were involved following decapitation.

Methods and Materials

The following method is essentially the one used by Wildman (1952) to induce callus and bud formation in decapitated tomato seedlings:

Seeds of *Lycopersicum esculentum* Miller (variety Bonnie Best), were sown in vermiculite. When the seeds had germinated, a modification of Schive's Complete Nutrient solution was added to the vermiculite. On the sixteenth day from the time of sowing, the plants were transferred to test tubes containing a preparation composed of agar and the modification of Schive's Complete Nutrient solution. No attempt was made to regulate the temperature or the humidity of the environment in which the seedlings were growing but the temperature on the average ranged above 20 degrees centigrade. The plants were given thirteen hours of illumination. This was accomplished by subjecting the plants to available daylight and fluorescent light during the day. After daylight hours, the plants were kept under fluorescent lights for the period of time necessary to make up the total of thirteen hours.

On the thirty-second day from the time of sowing, some plants were decapitated 7.5 mm above the cotyledon while others were permitted to grow without decapitation. A single application of lanolin (Anhydrous USP) was applied

to the cut surface of some plants while lanolin was not applied to the cut surface of others.

On the forty-third day after sowing, the buds developed in the axils of the cotyledons were removed.

Material for histological study which was collected at various intervals after decapitation was fixed in Craf III, aspirated, dehydrated, cleared in a TBA series and embedded in paraffin. The material was sectioned at 10, 13 and 17 microns and stained with Safranin O, Fast Green and Orange G.

GROSS OBSERVATIONS

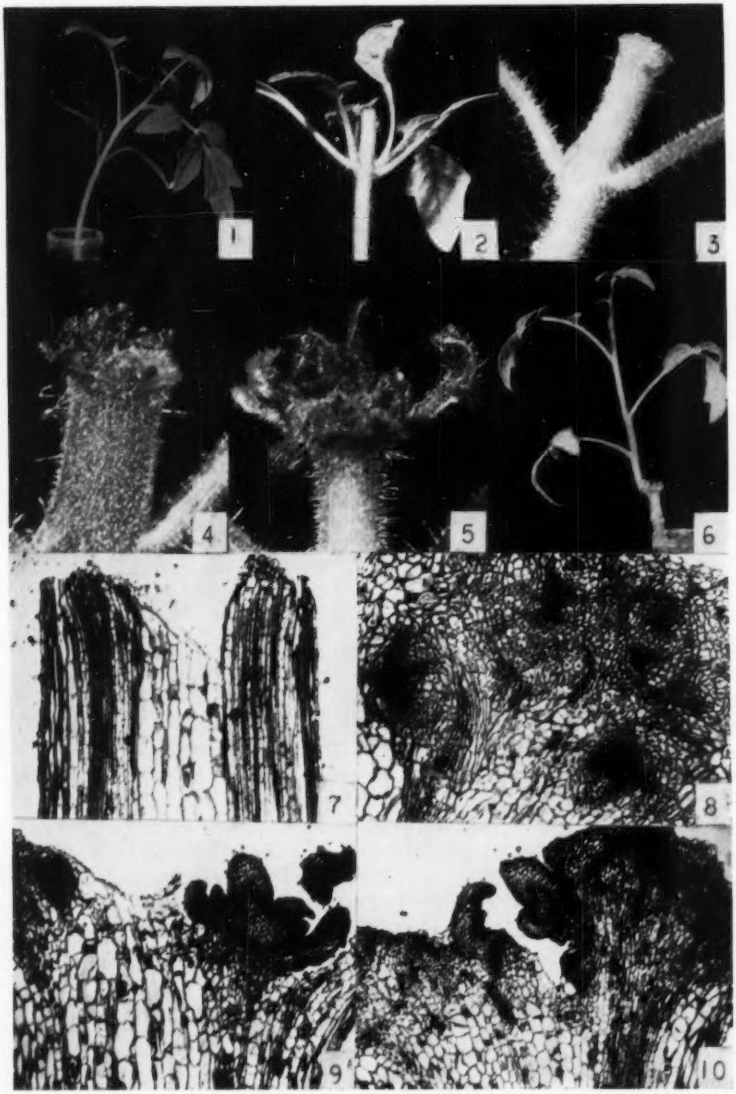
The seeds required approximately seven days for germination. At the time the plants were transferred from vermiculite to agar, the cotyledons were well spread and the primary leaf was conspicuous. Between the sixteenth and thirty-second day, the hypocotyl of the plants became reddish in color and this color persisted throughout the entire observation peirod, but became lighter after the plants were decapitated.

At the time of decapitation (fig. 1) the distance between the cotyledons and the first leaf ranged between 2.0 and 3.9 cm. Most plants at this time had three leaves and in some instances, a fourth. The cotyledons of most of the plants at the time of cutting appeared chlorotic, but three or four days after treatment the cotyledons developed more green pigment. The cotyledons remained on the decapitated plants during the entire observation period while many of the control plants lost their cotyledons by the thirty-sixth or thirty-seventh day from the time of sowing.

On the second day after decapitation, white spots appeared on the cut surface of the stem treated with lanolin. Eventually a callus developed; at the same time axillary buds also developed (fig. 2) between the remaining epicotyl and the cotyledons, so that by the eleventh day from the time of decapitation, these buds were 2.0 to 4.0 cm in length. The callus formed over most of the cut surface of the epicotyl, except at the very center, to the extent that it overlapped the epidermis (fig. 3). About three days after the axillary buds were removed, small purple strands and buds appeared on the surface of the callus (fig. 4). These purple strands developed into leaves of various shapes and sizes, while the buds produced stems. Some plants produced leaves and no stems while others produced both. Few of the leaves developed to any great extent. Many died relatively soon leaving only one to three leaves on the epicotyl. In those cases where both leaves and stems developed, the leaves appeared first (fig. 5). As the stem grew most of these first leaves died. The newly formed stem resembled the stem of the normal plant (fig. 6).

MICROSCOPIC OBSERVATIONS

Anatomy of the Epicotyl at Time of Cutting.—Transverse and longitudinal sections of the stem at the time of cutting reveal that the epidermis is a single row of cells almost uniform in size and shape with occasional epidermal hairs projecting from some of them. These hairs are of two types: short unicellular hairs and longer multicellular ones which are stalked and terminated with four or more glandular cells. The chlorenchyma, immediately inside the epidermis, is a narrow zone of loosely arranged cells. The collenchyma is a well developed zone several cells thick which forms a continuous



Figs. 1-10.—1. The tomato plant at the time of decapitation; 2. A decapitated plant showing the axillary shoots eleven days after decapitation; 3. A decapitated plant showing a callus on the wounded surface thirteen days after decapitation. Note that the axillary shoots are removed; 4. A treated plant nineteen days after decapitation. Buds and leaf primordia are visible on the surface of the callus; 5. A treated plant twenty-seven days after decapitation showing leaves growing above the wounded surface of the epicotyl; 6. A stem which developed from one of the buds differentiated from the callus; 7. Photomicrograph showing the disintegrated pith and also the formation of the protuberances which

layer around the stem. The cells are isodiametric in transection and the thickened angles of the walls of these cells are very pronounced. The length of the cells is ten to fifteen times the diameter. Centripetal to the collenchyma is a layer of parenchyma, the cells of which are thin-walled and rather long and wide. The endodermis is one cell in thickness and is composed of thin-walled cells which resemble the parenchymatous cells centripetal to the collenchyma except for the presence of starch grains. Casparian strips are not visible in either longitudinal or cross sections.

The vascular tissue is composed of six patches of primary xylem situated around the pith and several areas of internal and external phloem which are not necessarily found in direct association with the patches of xylem. The phloem is thus arranged as scattered strands in two cylinders. Several layers of uniform rectangular cells and a cambial zone which is in the first stage of division separate the external phloem from the lignified xylem. The external phloem groups are separated from each other and from the endodermis by parenchymatous cells which are irregular in size and constitute the pericyclic region of the stele. The tracheary elements of the primary xylem are thick-walled and are separated by parenchymatous cells. The protoxylem consists of narrow, distorted, ringed and spiral elements while the metaxylem elements are reticulate. The phloem is composed of small groups of sieve tubes with their companion cells and parenchyma. Nuclei are especially prominent in the narrow companion cells associated with these sieve tubes. The pith is a region several cells wide composed of thin-walled cells. These are the largest cells found in the epicotyl.

Anatomy of the Epicotyl Following Decapitation.—The response of the epidermis to decapitation is a slight enlargement of the cells causing it to be pulled away from the chlorenchyma producing large intercellular spaces. These spaces are very pronounced in some sections.

The chlorenchyma begins to enlarge about three or four days after treatment and by the twelfth day after treatment, the cells have enlarged two or three times the size of those found in the normal stem. These cells are also stretched and ruptured so that in many instances it is difficult to determine their shape. Chloroplasts are very numerous and prominent in the chlorenchyma cells of the treated plants while those found in the cells of the untreated plants are neither as numerous nor as outstanding.

The collenchyma shows little or no response to treatment except for slight enlargement.

The parenchymatous cells centripetal to the collenchyma start to enlarge four or five days after treatment. Older sections reveal that these cells have enlarged one and one half times the size of the cells found in the untreated stem. Occasionally, periclinal divisions occur and sometimes anticlinal divisions are observed, but on the whole these cells are never in an active state of division.

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are located above the cut surface in the vicinity of the vascular tissue. 20.6×; 8. A longitudinal section of the callus showing several areas of meristematic activity. 60×; 9. A longitudinal section of treated epicotyl through the callus showing two stem tips which have differentiated from the callus tissue. 20.6×; 10. A longitudinal section of epicotyl sixteen days after decapitation in which the general topography and also a leaf primordium can be observed. 20.6×.

Figs 11-18.—11. A longitudinal section showing the protuberances from the xylem and phloem parenchyma. 60×; 12. A longitudinal section showing the division of pith cells. 60×; 13. A section through the callus showing the differentiation of the tissue into leaf primordia. 60×; 14. A transverse section of the callus above the cut surface showing that in reality the callus is a ring of cells. 20.6×; 15. A stem tip differentiated from the callus. 60×; 16. A leaf differentiated from the callus showing the provascular strand. 57.6×; 17. A longitudinal section showing the formation of xylem from parenchymatous cells in vicinity of internal phloem. 60×; 18. A longitudinal section showing detail of xylem differentiating from parenchymatous tissue in vicinity of internal phloem 209.5×.

The cells of the endodermis show no striking change after treatment. Occasional periclinal divisions are seen and the cells appear to have enlarged about one and one half times the size of the cells found in the untreated stem. The number of starch grains in the endodermal cells of the treated stems decreases so that by the end of the experimental period, some endodermal cells are completely void of starch grains.

Five or six days after treatment, the most striking changes occur in the vicinity of the vascular tissue. The cells of the xylem and phloem parenchyma near the immediate surface react to wounding by protruding above the cut surface to form the beginnings of a callus (figs. 7, 11). These callus cells which eventually cover the surface of the treated stem only in the vicinity of the vascular tissue are highly vacuolate, contain a nucleus and have no definite shape except that most of them have rounded corners giving them the appearance of misshapen spheres. These early projections divide and are eventually pushed upward by the tissue from below.

The cells in the proximity of the vascular tissue about three or four cells below the surface also react to treatment in the same way as those cells at the surface. The protuberances, however, break through the adjacent cell walls. Some of the protuberances do not necessarily rupture the cell walls of the adjacent cells but displace the adjacent cells as they grow between them.

Below this area of activity, the xylem and phloem parenchyma becomes rich in cytoplasm and begins to divide at first periclinally, then anticlinally and eventually in all planes to form masses of compact cells. Divisions are very frequent and numerous causing a displacement of the various tissues found in their immediate proximity. These compact masses of newly formed cells displace the rigid tracheary elements which become broken into segments. As the divisions become more numerous there is outward growth of these cells towards the surface which eventually forms masses of meristematic tissue above the cut surface of the stem (figs. 8, 9, 10, 13). Segments of the displaced tracheary elements are carried with the upward growth and are seen in the midst of the newly formed tissue. A median longitudinal section of the stem shows two fan-shaped masses of callus cells, one on either side of the pith (fig. 9). In reality this is a ring of newly formed cells (fig. 14).

As divisions are occurring in the vicinity of the vascular tissue, some of the pith cells at the center near the surface die (figs. 9, 12). The walls of these cells stain red with safranin possibly because of suberization (fig. 12). Even though the pith as a whole never shows considerable activity, some of the cells near the surface in the vicinity of the xylem and phloem divide in all planes and their derivatives grow upward above the cut surface as in the case of the derivatives of the xylem and phloem parenchyma (fig. 12). Thus the derivatives of the xylem and phloem parenchyma plus the derivatives of the pith cells adjacent to the vascular tissue comprise the callus (fig. 14).

The cells of this callus are very compact, without intercellular spaces and are of no definite shape or size (fig. 13). They are not vacuolate and the nuclei and nucleoli are generally large in comparison to the size of the cells. From one to five spherical red staining bodies of various sizes are observed in the cytoplasm of these callus cells. These spherical bodies appear to be solid, hyaline, and homogeneous. As differentiation of the callus tissue occurs, the number of

spherical bodies in each of the cells diminishes and eventually the cells become entirely void of them.

About twenty days after cutting, many areas of differentiation can be observed in stained sections of the callus tissue (fig. 8). Some areas of differentiation are spherical nests of meristematic activity, while other areas have various shapes. In some instances, some of the callus cells enlarge and differentiate into tracheids (fig. 8) while some of the areas of meristematic activity give rise to stems and leaves (figs. 9, 10, 13, 16).

The stem tips which are differentiated from the callus tissue (figs. 9, 15) in general topography differ from the stem tips of the untreated plants in that the former are more peaked. The cells comprising the regenerated stem tip in general appear to be larger than the cells found in a normal stem tip. However, like the normal one, the embryonic region of regenerated stem tip is covered by a single layer of cells which corresponds to the tunica described by Eames and MacDaniels (1947) and a central region composed of highly vacuolate cells flanked on either side by cells which are more dense in cytoplasm. Transverse sections of newly formed leaves reveal that internally they are structurally similar to the leaves found on an untreated plant.

As differentiation of the callus tissue into leaves and stems is occurring, some of the parenchymatous cells adjacent to internal phloem below the wounded surface differentiate into tracheids (figs. 17, 18). These parenchymatous cells start their development into xylem elements by enlarging and when the cells reach their full diameter, the end and longitudinal walls develop secondary thickenings of the reticulate and scalariform type. When the protoplast disappears and the longitudinal secondary walls are mature, the end walls of the cells disappear to form a vessel. The fact that these cells first expand, disrupts the adjacent cells so that they become distorted and cause an actual tearing of the tissue in the immediate vicinity. In transverse sections, these newly formed tracheids appear in the form of bundles within the pith. The xylem elements which differentiate from the callus and those which differentiate from the parenchymatous cells near the internal phloem initiate a new vascular system which connects the newly formed shoots with the vascular system of the epicotyl.

DISCUSSION

Botanists who have been concerned with the physiology of development have considered living plants to be in part, expressions of the environment. They believed that any living cell with proper stimulation is capable of renewed meristematic activity. This viewpoint has been substantiated by many investigations on the response of plants to wounding, to growth substances and to environmental changes. For example, the investigations of Kraus et al. (1936) and Borthwick et al. (1937) show that practically any living cell is capable of renewed meristematic activity. Their histological observations show that the epidermis, collenchyma, cortex, phloem and xylem parenchyma and even pith were capable of becoming meristematic after the application of growth substances. Even before the extensive use of growth substances it was shown that buds may develop from cells of the epidermis, cortex, pericycle, xylem and phloem parenchyma and pith after the formation of a callus (Simon 1908).

The present study also adds to the evidence that bud primordia may develop from the renewed activity of the cells of the xylem and phloem parenchyma and pith cells, after callus formation.

The adventitious buds and the leaf primordia which were produced under the conditions of this study show that the primordia are produced in the callus which was formed from the proliferation of the cells of the xylem and phloem parenchyma and pith cells adjacent to the xylem and phloem. The cells of this callus become organized nests of activity that give rise to stem tips and leaf primordia. This cellular organization within the callus before the formation of primordia has been shown by Küster (1903) and Rechinger (1894).

SUMMARY

Seedlings of *Lycopersicum esculentum* Miller which are decapitated above the cotyledons and treated with lanolin produce a callus on which leaf primordia and buds frequently develop. The first response to wounding observed in plants is an enlargement of the cells of the epidermis, cortex and pith. The pith cells at the immediate surface of wounded stem disintegrate and appear to become suberized. The most striking response to wounding is in the vicinity of the vascular tissue. The cells of the xylem and phloem parenchyma near the immediate surface protrude above the cut surface to initiate callus formation. The cells of the xylem and phloem parenchyma below the cut surface also protrude and cause damage to the adjacent cells. Cells of the internal and external phloem parenchyma and xylem parenchyma become rich in protoplasm and divide in all planes to form compact masses of tissue which are eventually pushed upward. The rigid tracheary elements near this area of activity are displaced and are carried with the upward growth. The cells of the pith near the internal phloem also proliferate to form compact masses of cells which protrude above the surface. The callus is the result of the proliferation of the cells of xylem and phloem parenchyma and the proliferation of the pith cells adjacent to the internal phloem.

The callus is composed of cells which are compact, are of no uniform shape or size, and are not vacuolate. Red staining spherical bodies are observed in the callus and the number of spherical bodies diminishes as differentiation is occurring.

Twenty days after decapitation, many areas of differentiation are seen in the callus tissue which appear as circular nests of activity. Some of these areas of activity give rise to stems and leaves. Some cells differentiate into xylem elements.

Stem tips which are differentiated from the callus tissue differ from the stem tip of untreated plants in that the former are more peaked. The normal one resembles a flattened dome. The leaves formed on plants decapitated above the cotyledons appear to be flattened appendages of various shapes and sizes. Transections show that they are structurally similar to the leaves of an untreated plant.

Some of the parenchymatous cells of the internal phloem below the wounded surface differentiate into xylem elements as differentiation is taking place in the callus tissue above. In transverse section, the newly formed tracheary elements appear in the form of bundle within the adjacent pith.

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Hybridization Between the Perennial Sunflowers Helianthus salicifolius A. Dietr. and H. grosseserratus Martens[1]

Robert W. Long, Jr.[2]
Ohio Wesleyan University, Delaware

The genus *Helianthus* L. presents many problems in plant systematics, and questions in delimiting sunflower species are raised by professional and amateur botanists alike. Sunflowers are annuals or perennials, with a few shrubby forms in tropical America (Watson, 1929); approximately 90% of the species are perennial. Little work on perennials has been reported, although Heiser (1951) has contributed greatly to our understanding of the annuals.

One of the more distinctive species of the genus is *H. salicifolius* A. Dietr. (*H. orgyalis* DC). It is a series of populations characterized by smooth, glaucous stems bearing crowded, sessile, lance-linear, entire leaves (fig. 2a), with terminal panicles of yellow or brown disks. It has a somewhat restricted distribution, chiefly over the central prairie region of Missouri and Nebraska, Arkansas, Oklahoma, and parts of Texas (fig. 1). The species often occurs in limestone soils, and frequently appears as dense plumes of long, narrow leaves which completely hide the stem (Watson, 1929).

Fig. 1.—Distribution of *Helianthus salicifolius, H. grosseserratus,* and reported collections of the hybrid, *H. Kellermanni.* Dashed lines, *H. salicifolius;* stipuled area, *H. grosseserratus;* arrows, location of collections of *H. Kellermanni.*

Helianthus grosseserratus Martens is common within its range, and is usually characterized by its tall, stout, smooth stems bearing large, lanceolate to lance-ovate, long-petioled, strongly serrate leaves (fig. 2c), with a terminal panicle of heads with yellow disks. It is distributed over a wide area, ranging from New York to Iowa and Texas (fig. 1). Unlike *H. salicifolius,* it occurs in many soil types, principally in rich, well-drained soil.

[1] The study here reported was done at Indiana University where investigations regarding the cytogenetics and taxonomy of sunflowers are in progress.

[2] *Acknowledgment.*—The author expresses appreciation to Dr. C. B. Heiser of Indiana University for his interest and suggestions during the progress of the study. Thanks are due to Drs. L. H. Shinners and S. W. Geiser of Southern Methodist University for their helpful suggestions in the preparation of the manuscript.

Fig. 2.—Typical leaf outlines of (A) *H. salicifolius*, (B) *H. Kellermanni*, and (C) *H. grosseserratus*. Approximately × 1/4.

Helianthus Kellermanni Britton (figs. 2b, 3a) was named after its founder who had discovered it growing near Columbus, Ohio (Britton, 1901). Since the original collection it has been reported only rarely, and Fernald (1950) describes it as occurring locally from eastern New York to Ohio and Wisconsin (fig. 1). The hypothesis that *H. Kellermanni* was a hybrid or hybrid derivative of *H. grosseserratus* and *H. salicifolius* (fig. 3b) was first advanced by Cockerell (1919), and Gleason (1952) also interprets the "species" to be a hybrid. The close morphological relationship of *H. Kellermanni* to *H. grosseserratus* was noted in the single clone of the former that was obtained from Dr. C. C. Deam, originally from Columbus, Ohio, for the experimental gardens of Indiana University.

The hypothesis that *H. Kellermanni* was not a valid species was tested by means of crossing experiments and cytological observations. In 1951 successful initial crosses using *H. Kellermanni* (p60) and a race of *H. grosseserratus* (p78) demonstrated the interfertility of the two; vigorous F_1 progeny were produced. Pollen fertility was tested by staining microspores with cotton-blue in lactophenol. *Helianthus gosseserratus* had 83.0-98.3% viable pollen; *H.*

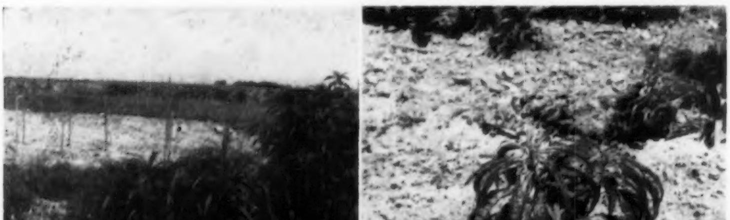

Fig 3.—a. Natural hybrid, "*Helianthus Kellermani*" (p60). b. Artificial hybrid, *Helianthus grosseserratus* × *H. salicifolius*.

TABLE 1.—Garden races used in study.

Species	Code	Collector	Source
grosseserratus	p78	C. B. Heiser	Belleville, Ill.
grosseserratus	p3118	C. B. Heiser	Bloomington, Ind.
grosseserratus	p46-1	J. Magee	Black Hawk Co., Ia.
grosseserratus	p46-2	J. Magee	Black Hawk Co., Ia.
salicifolius	p115	Pearce Seed Co.	Unknown
Kellermanni	p60	C. C. Deam	Columbus, Ohio

Kellermanni had 39.6-58.0% viable pollen. Hybrids showed pollen fertility ranging from 65.0-69.5%.

More extensive crossing experiments were made in the two succeeding summers using additional races of *H. grosseserratus* with *H. Kellermanni* and *H. salicifolius*. Table 1 lists the races used in the study. Vigorous hybrids were produced no matter in which direction the cross was made. It was noted, however, that the F_1 progeny of *H. grosseserratus* × *H. salicifolius* were generally uniform, typical for the first hybrid generation, and were closely similar to *H. Kellermanni*. Pollen fertility for these hybrids ranged from 41.0-64.2%. On the other hand, the F_1 progeny of *H. grosseserratus* × *H. Kellermanni* and *H. salicifolius* × *H. Kellermanni* showed many individual variations, results more typical of backcross and F_2 generations. Table 2 lists the morphological features of the garden races.

Fig. 4.—Meiotic chromosomes of *H. grosseserratus*, *H. Kellermanni*, and hybrids at Metaphase I. (A) *H. grosseserratus*, 17 bivalents; (B) *H. Kellermanni*, 17 bivalents; (C) *H. grosseserratus* × *H. Kellermanni*, circle of four and 15 bivalents; (D) *H. grosseserratus* × *H. Kellermanni*, chain of four and 15 bivalents. Approximately × 350.

Cytological studies were made on microsporocytes using the acetocarmine squash technique on buds fixed in acetic acid-absolute alcohol solution, one part acid to three parts alcohol (fig. 4). The haploid chromosome number for *H. grosse-*

TABLE 2.—Comparison of Morphological Features of Garden Races in Study

	grosseserratus (see table 1)	*salicifolius* (p115)	*grosseserratus* × *salicifolius*	*Kellermanni* (p60)
Stem				
height	3.0-3.5 m.	2.0-2.2	2.0-3.0	2.0-2.5
Leaf (low cauline)				
shape	lance-ovate	lance-linear	narrowly lanceolate	narrowly lanceolate
length	31.0-34.0 cm.	17.0-19.2	34.0-35.5	26.0-32.0
width	7.9-8.0 cm.	0.2-0.5	1.8-2.5	2.0-2.8
margin	deeply serrate	entire	irregularly serrate	irregularly serrate
undersurface	white tomentose	subglabrous	scattered short hairs	scattered short hairs
petiole	5.4-5.6 cm.	subsessile	0.8-0.9	0.5-0.7
Head				
phyllary	2.2 cm.	2.4	2.2-2.3	2.0-2.1
ligule	3.5 cm.	2.0-2.1	2.5-2.6	2.5-2.6
disk diameter	1.7-1.8 cm.	1.0	1.5	1.2-1.3

serratus, H. salicifolius, and *H. Kellermanni* is seventeen, as reported by Heiser (1949). In twenty-two cells studied at meiosis in *H. Kellermanni,* two cells contained chromosome chains and univalents. Similar types of chromosomal configurations were noted in the *H. grosseserratus* × *H. salicifolius* hybrids, but meiotic irregularities in races of *H. grosseserratus* and *H. salicifolius* are rare.

Herbarium material of *H. Kellermanni* was obtained from the Gray, Indiana University, and Michigan State herbaria. In all cases excepting the type collection, the specimens had been grown in cultivation and not collected from natural populations. However, of the twelve sheets examined of *H. Kellermanni,* four plants showed notable variations in phyllary and leaf characteristics from the type. In these cases the phyllaries were loose and more linear attenuate, resembling *H. salicifolius.* One specimen had leaves almost tomentose below, resembling *H. grosseserratus.*

Both *H. salicifolius* and *H. grosseserratus* are occasionally cultivated as ornamentals for their smooth leaves and bright yellow inflorescences. *Helianthus salicifolius* is listed by some seed companies, and produces tall, delicate, handsome plants. Specimens of this species recorded as collected in the northeastern and north-central states can be attributed to garden varieties or escapes.

We can conclude that *H. Kellermanni* is not a series of natural populations with distinctive geographical, morphological, and genetic characteristics, but rather a sporadically occurring hybrid or hybrid derivative of *H. grosseserratus* and cultivated *H. salicifolius* growing within the range of the former. *Helianthus Kellermanni* behaves as a hybrid in crossing experiments, producing segregating F_1 progeny when hybridized with both *H. grosseserratus* and *salicifolius* and showing some meiotic irregularities in microsporogenesis. Finally, *H. Kellermanni* is closely similar to the artificial hybrid *H. grosseserratus* × *H. salicifolius,* corresponding to the hybrid in practically all characteristics.

The importance and role of natural hybridization in perennial sunflowers has yet to be evaluated, but there is little doubt as to its occurrence (*cf.* Cockerell, 1929). The ease of crossing in these garden races of the present study might well be indicative, for certainly *H. grosseserratus* and *H. salicifolius* are morphologically distinctive, yet they form vigorous, partly fertile hybrids when crossed.

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Effects of Rapid and Ultra-Rapid Freezing on Trichinella spiralis larvae from Guinea Pigs and Rats[1]

Robert J. Shaver
Dow Chemical Co., Midland, Michigan

John D. Mizelle[2]
University of Notre Dame, Notre Dame, Indiana

Experimental work concerning effects of low temperatures on the larvae of *Trichinella spiralis* began almost one hundred years ago (Leuckart, 1863 *from* Ransom, 1916). Prior to 1914, it was generally accepted that these larvae were very resistant to cold. Ransom (1916) showed that low temperatures exert a very pronounced effect on the vitality of these parasites. Augustine (1933), Blair and Lang (1934), and Gould and Kaasa (1949) pointed out that early workers, including Ransom (1916), worked mainly with air temperatures prevailing outdoors, or in ordinary cold storage compartments in which the rate of temperature change of infected meat was relatively slow. With the advent of rapid-freezing methods, van Thiel (1925), Augustine (1933), Blair and Lang (1934), and Gould and Kaasa (1949) reinvestigated previous findings in an attempt to determine the low temperature and period of exposure necessary to kill encysted larvae of *Trichinella spiralis*. The results of these workers are summarized by Gould and Kaasa (1949) and are discussed later in this work. Since Shaver (1953) indicated that motility of larvae after subjection to rapidly attained low temperatures was not a criterion of viability, some previous works may be questioned.

The purposes of the present investigation were 1) to determine the role played by the method of infection as revealed by the presence of second-generation larvae in the diaphragm of experimental rats; 2) to determine the efficiency of the trichinoscope as a means of counting accurately the number of larvae in infected muscle; 3) to test the comparative resistance of *T. spiralis* larvae to low temperatures; 4) to compare the viability after subjection to low temperatures, of *T. spiralis* larvae from rats and guinea pigs and to test the susceptibility of these two hosts to this parasite; 5) to determine the role that thawing procedures play in regard to motility and infectivity of the larvae; 6) to determine the protection provided *T. spiralis* larvae by dehydration in glycerol prior to subjection to low temperatures; and 7) to test the effect of storage in normal saline at 3°C on the motility and infectivity of *T. spiralis* larvae.

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[1] Contribution from the Department of Biology, University of Notre Dame, Notre Dame, Indiana.

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MATERIALS AND METHODS

The rats used in these experiments were reared and maintained on Rockland Rat Diet (complete)[3]. The guinea pigs used were reared and maintained on Nappanee Rabbit Pellets.[4] Both diets were supplemented with green leafy vegetables.

Food was withheld from hosts for twelve hours prior to, and from ten to twelve hours after ingestion of experimental larvae. A known number of larvae were administered by means of a 3 ml Luer-Lok syringe and an attached catheter which was passed into the stomach of the ether-anesthetized host.

When rat or guinea pig diaphragms were to be subjected to low temperatures, the infected hosts were killed and the diaphragms removed and spread on the outer surface of petri-dish covers which had been stored at the experimental temperature to be used. Then the diaphragms were pressed between the petri-dish cover and the floor of a refrigerator frost chest with a two-pound weight. Exposure was measured from contact with, to removal of the diaphragms from, the frost chest surface. The muscle was thawed either by 1) immersion in saline (0.9% NaCl) or 2) in air at room temperature, and digested[5] to liberate the larvae.

Larvae freed by artificial digestion and to be dehydrated in 50% glycerol, before subjection to low temperatures, were treated as follows: a known number of larvae were isolated in the depression of a spot plate with the aid of a dissectoscope; the saline was removed with a micropipette and filter paper. A solution of 50% glycerol was added to the larvae in the depression and allowed to remain for five minutes. The larvae were then transferred to a glass cover slip with a micropipette and all but a thin film of the glycerol was removed with filter paper. The cover slips were then placed against the floor of the frost chest, or inserted between two blocks of dry-ice (8 x 4 x 1 in.), or rapidly immersed in liquid nitrogen contained in a Dewar flask.

Counts and observation of motility were made on experimental larvae, after liberation by digestion, in saline at 37.5°C, utilizing a depression spot plate and a dissectoscope. Non-motile larvae were examined also under the low- and high-power objectives of a compound microscope.

The temperature-control switch of the refrigerator was "by-passed" and with the refrigerator running continuously, temperatures from -16 to -34°C were readily obtained. Blocks of dry-ice provided a temperature of -78.5°C within twenty seconds. This time lapse is thought to be due to the inability of the Brown potentiometer to record the extremely rapid drop in temperature. A temperature of -196°C was obtained with liquid nitrogen

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[3] Rockland Farms, Arcady Farms Milling Co., Chicago, Ill.

[4] Nappanee Milling Co., Nappanee, Ind.

[5] Hill's (1951) method of macerating (in a Waring blendor) and screening trichinous muscle was used to isolate the encysted larvae. The cysts and small fibers of muscle containing cysts were then subjected to artificial digestion in large flasks and the freed larvae collected by Hill's (1951) sedimentation technique. The N/10 sodium hydroxide utilized by Hill as a clearing agent was not employed because of its possible deleterious effects on the larvae. Schwartz's (1939) digesting fluid, which was also used by Hill, consisted of scale or spongy pepsin (U.S.P.), 5-6 grams; HCl (conc.), 10 ml; water, 600 ml. Digestion was accomplished at 37.5°C in 3-4 hours with periodic shaking.

TABLE 1.—Larvae encysted in diaphragm of test rats after 100 larvae were fed to each. Diaphragms examined 30 days after infection.

	Number of larvae recovered	
Capsule-fed	Diaphragm-fed[7]	Syringe-fed
141	504	137
171	368	104
290	718	91
107	799	189
109	689	111
307	598	166
232	829	63
134	684	66
337	failed to eat diaphragm	84
292	390	98
Totals 2120	5579	1109
Av. 212	620	111
	461 (corrected)	

in five seconds; three seconds after immersion of the coverglass, the temperature was approximately -180°C. Temperatures from -16 to -78.5°C were measured and recorded by a Brown Recording Potentiometer, Minneapolis, Honeywell Co., Philadelphia. The temperature of liquid nitrogen was measured with a Rubicon Potentiometer, Rubicon Co., Philadelphia. Thermocouples of constantan and copper wires (0.25 mm in diameter) were used with both potentiometers.

A trichinoscope, very similar to that used by the National Institutes of Health (Gould, 1945: 170), was used to determine the efficiency of the "trichinoscope *vs.* the artificial digestion method" in counting larvae in the experimental host diaphragms.

EXPERIMENTS AND OBSERVATIONS

Experiment 1 was designed to determine the effect of the manner of infection as interpreted by the presence of encysted second-generation larvae in the diaphragm of the rat. Ten rats were sacrificed forty days after infection.[6] Pieces of diaphragm containing approximately one hundred larvae (counted with trichinoscope) were given to each of ten young adult male rats, all but one of which ate the material. The remaining muscle was digested and one hundred of the recovered larvae contained in a sealed gelatin capsule, were force fed to each of ten young adult male rats, and 100 larvae in 1 ml of normal saline were given to each of ten young adult male rats by means of a syringe and catheter. These three groups of test rats were sacrificed thirty days after infection and the larvae were counted.

The results of this experiment (table 1) indicate that nearly six times as many larvae encyst in the diaphragm of rats when fed infected diaphragm as compared with results after infection by the same number of larvae with

[6] The age of the infection cited herein are reckoned from the time of ingestion of infective larvae.

[7] Larvae counted in diaphragms were as follows (reading from top): 105, 100, 99, 111, 100, 101, 98, 90, 94, 96.

a syringe, and nearly three times that obtained by capsule feeding. Experiment 2 shows that approximately one-fourth of *T. spiralis* cysts in 40-day-old infections are not detected by the trichinoscope. After correction of the value for diaphragm-fed larvae utilizing this factor (25.72), the number of larvae in infections produced by this method (461) is more than twice that for capsule-fed (212), and more than four times that (111) for the syringe-fed, infections. It should be noted that there are other variables which may account for such discrepancies of second generation larvae: 1) male-female ratio, 2) number of females inseminated, 3) number of larvae produced by each gravid female ("probably about 1500 per female", Hyman, 1951:384, Chandler, 1949:381; "approximately 1000", Gould and Kassa, 1949), 4) variation in number of larvae localizing in the diaphragm, 5) individual resistance and variability offered by each host, 6) age and/or degree of calcification of infecting larvae.

Ransom (1916) demonstrated that artificial digestion for twenty-four hours or less has no appreciable effect upon the vitality of trichinae. According to Gursch (1948) four to eight hours of digestion does not impair the infectivity of *T. spiralis* larvae, but that a twelve-hour period of digestion decreased the percentage of worms recovered from test infections. The larvae used in the above experiment were recovered after digestion of diaphragms for three to four hours and no damage is thought to have occurred. A stomach tube (syringe and catheter) has been used to feed larvae to rats

TABLE 2.—Efficiency of the trichinoscope *vs.* the digestion method in determining the number of *T. spiralis* larvae in the rat diaphragms.

Rat No.	Count of larvae in diaphragm: Trichinoscope	Digestion	Difference
	40 days after infection		
1	259	311	52
2	196	277	81
3	303	508	205
4	337	469	132
5	251	285	34
6	285	442	157
7	167	208	41
8	137	153	16
9	173	185	12
10		Died while feeding	
Totals	2108	2838	730
	140 days after infection		
1	48	56	8
2	45	50	5
3	18	27	9
4	24	32	8
5	137	149	12
6	93	108	15
7	229	283	54
8	240	294	54
9	37	56	19
10	17	30	13
Totals	888	1085	197

TABLE 3.—Effect of a two-minute exposure at -16°C and thawing in different media, on 70-day-old *T. spiralis* larvae, as shown by the number of larvae recovered from rat diaphragms after 30 days.

Number of larvae recovered after thawing in			
Normal saline (37°C)	Digestive fluid (37°C)	Air (22°C)	Controls
761	172	56	871
808	221	890	564
778	501	10	201
256	148	0	54
died during feeding	5	376	432
Totals 2603	1047	1332	2122

by many previous workers (Augustine, 1933; Gursch, 1948; Gould and Kaasa, 1949) and is considered reliable.

Experiment 2 was designed to test the efficiency of the trichinoscope.[8] Ten of twenty heavily infected rats were sacrificed 40 days after infection, the remaining ten when the infection was 140 days old. Diaphragms were removed and the larvae were counted with aid of the trichinoscope. The material was then digested and the liberated larvae were counted. The data (table 2) reveal that the trichinoscope is only 74.28% efficient for determining 40-day-old trichinae infections, and only 81.84% efficient for 140-day infections. These findings agree with Gould (1945) who stated that "trichina cysts which are not calcified are more difficult to detect (with a trichinoscope) because of their transparency".

Experiment 3 was conducted to determine the effects of a two-minute exposure at -16°C on 70-day-old larvae of *T. spiralis* and the effect of the thawing procedure on the motility and infectivity of these larvae. Fifteen rats were heavily infected with *T. spiralis* and sacrificed 70 days later, at which time the diaphragms were subjected to -16°C for two minutes. Diaphragms of five animals were thawed immediately in normal saline at 37.5°C; those of another five were thawed immediately in artificial digestive juice at 37.5°C; diaphragms from the remaining five rats were thawed in air at room temperature (22°C). The larvae recovered from each diaphragm were observed for motility at 37.5°C, and one hundred-fifty pooled larvae from a given group were fed to each of five 50-day-old rats. Five 50-day-old rats were fed one hundred-fifty untreated larvae as controls. These twenty rats were autopsied when the infections were thirty days old and the recovered larvae counted (table 3).

Shaver (1953) demonstrated one hundred percent lethality after exposure of *T. spiralis* larvae to -16°C for three minutes but found that this temperature was not lethal after a one-minute exposure. The production of infections by feeding larvae recovered from diaphragms exposed for two minutes at -16°C demonstrates the margin of safety afforded by this exposure to be extremely narrow. One hundred percent of these experimental larvae, regardless of the thawing procedures, exhibited motility at 37.5°C. Of the three

[8] According to Chandler (1949) larvae begin to encyst about one month after infection. The cysts, at first very delicate, are not fully developed until after 7 or 8 weeks.

procedures used (table 3), thawing in normal saline permitted greater infectivity since the number of larvae recovered after its use was approximately 2½ times that obtained after thawing in artificial digestive fluid, approximately twice that obtained after thawing in air and one-fifth (22.67%) more than those obtained in the controls.

Experiment 4 was planned 1) to test the resistance of well-established (217 days) larvae of *T. spiralis* from guinea pigs and rats to -22°C for one minute and 2) to determine the effect of the thawing procedure on the motility and infectivity of the treated larvae. Five each of trichina-infected rat and guinea pig diaphragms, exposed to -22°C for one minute, were thawed in normal saline at 37.5°C and the same number from rats and guinea pigs (identically treated) were thawed in air at room temperature (22°C). The diaphragms were digested and the percentage motility of the recovered larvae was observed in normal saline at 37.5°C. One hundred larvae from a given diaphragm were fed to a young adult female rat in each case. Ten control rats were each fed one hundred untreated larvae from the rat host and five control rats were each fed one hundred untreated larvae from the guinea pig host. These were autopsied when the infections were thirty days old and the recovered larvae counted (table 4).

Eighty-six percent of the larvae from the rat and 95% of the larvae from the guinea pig were motile when thawed rapidly in normal saline at 37.5°C, while 71% of the larvae from the rat and 87% of the larvae from the guinea pig were motile when thawed in air at room temperature (22°C).

Cold treated larvae from guinea pigs, although exhibiting a higher percentage motility than larvae from the rat host, produced no infections in test rats. The number of larvae recovered from the control infections for guinea pig material was as follows: 43, 30, 119, 231, 47; a total of 470. All experimental larvae from the rat host produced infections, regardless of the thawing procedure (table 4). It is obvious from this experiment that motility is not a criterion of infectivity since in addition to the foregoing, larvae thawed in air which exhibited a lower percentage motility, produced a greater overall number of larvae. It may also be concluded that the larvae encysted in rat muscle are more resistant to cold than larvae encysted in guinea pig

TABLE 4.—Second-generation *T. spiralis* larvae recovered from rat diaphragms 30 days after feeding 100 larvae subjected to —22°C for one minute and thawed in air (22°C) and normal saline (37.5°C).

	Number of larvae recovered	
Controls	Air thawed (22°C)	Saline thawed (37.5°C)
166	95	15
153	180	177
149	135	88
166	80	96
73	51	15
111	11	59
129	120	45
127	76	47
65	176	61
207	86	177
Totals 1346	1010	780

muscle. In contrast to experiment 3, air-thawed larvae produced more trichina cysts than did the saline-thawed larvae.

Experiment 5 was designed to test the resistance of 265-day-old infections of *T. spiralis* larvae to -32°C for one minute. As in the previous experiment, an attempt was made to determine the effects of the thawing procedure. The treated larvae were fed to rats and guinea pigs to observe which was the better test animal. Ten trichina-infected rat diaphragms after exposure to -32°C were thawed (five) in normal saline at 37.5°C and (five) in air at room temperature (22°C). The diaphragms were digested and the percentage motility of the recovered larvae was determined in normal saline at 37.5°C. One hundred pooled air-thawed larvae were fed to each of ten young adult female rats and each of five young adult female guinea pigs. The saline-thawed larvae were fed identically to an equal number of rats and guinea pigs. Ten rats and five guinea pigs were each fed 100 untreated larvae as controls. All animals were autopsied when the infections were thirty days old and the recovered larvae counted.

Fifty-one percent of the saline-thawed larvae were motile; none of the air-thawed larvae exhibited motility. Evidently slow thawing in air at room temperature, which took from three to four minutes, greatly reduces the motility of the larvae after subjection to -32°C for one minute. In experiment 4, after a one-minute exposure to -22°C, 86% of the larvae from the rat host were motile when thawed rapidly in normal saline and 71% exhibited motility when thawed in air at room temperature. The inability of both air- and saline-thawed larvae to produce infections in the present experiment, except in one case (slowly thawed in air; 14 larvae were recovered from the diaphragm of one rat) indicates a much lower resistance than that observed at a -32.2°C by Blair and Lang (1934). It must be assumed from this experiment that a one-minute exposure to -32°C is one hundred percent lethal to *T. spiralis* larvae (the 14 larvae recovered from one experimental animal are thought attributable to an error in procedure) even though some larvae were motile. The total number of larvae recovered from the control rats was 3,475 for the ten animals. Ninety-three larvae were recovered from the four control guinea pigs (one control died before the experiment was terminated).

Experiment 5 also indicates that the guinea pig, as an experimental host, is not as desirable as the rat. For *T. spiralis* the average number of larvae recovered from the diaphragms of the control rats was 347.5, over 15 times the average number recovered from the guinea pig.

The findings of van Thiel (1925), Augustine (1933) and Blair and Lang (1934) concerning the temperature necessary to kill larvae from guinea pigs do not agree with the results in the present work.

Van Thiel working primarily with small pieces of trichinous muscle from the guinea pig discovered that a temperature of -20°C, maintained for fifteen minutes was required to kill the larvae. When finely ground meat was thinly spread on a surface at the same temperature they were killed in five minutes.

Augustine (1933) inserted trichinous guinea pig muscle into the center of raw pork loin roasts (average weight four pounds) and rapidly lowered the temperature with a laboratory type Birdseye multiple plate freezer maintained at a temperature of -35°C. From four to six hours were required, depending on the temperature desired (-18.1 to -34.6°C) for the muscle to reach a

given temperature. Temperatures were determined by copper constantan termocouples inserted in the guinea pig muscle. Augustine (1933) reported that larvae apparently suffered no injury when subjected to -21°C for four hours. "They appeared normal upon microscopical examination, responded actively to heat stimulus, and heavy infections were produced in all the test animals (usually mice) fed either defrosted meat or isolated larvae." He reported that temperatures of -24.8 and -27.6°C appeared to affect the viability to some extent. The encysted larvae, when examined microscopically, appeared damaged, however, once digested from the muscle they appeared uninjured. Infections (noticeably lighter than those produced by larvae maintained at -21°C) resulted in all test animals when encysted or freed larvae were fed. A temperature of -30.9°C profoundly lowered the viability of the larvae in four hours and 33 minutes. A few isolated larvae remained coiled, appeared normal and responded sluggishly to warmth. "Only very slight infections resulted in about half the test animals fed this material." When the larvae were subjected to a temperature of -33.7°C for 5 hours and 10 minutes, a few responded to warmth but no infections resulted when they were fed to test animals. Augustine (1933) observed no living larvae in trichinous meat subjected to a temperature of -34.6°C for 6 hours and 1 minute, nor were any infections produced by feeding. Samples were also cooled to -18°C in approximately four hours and then stored at this temperature for fourteen, twenty-four, and thirty-nine hours respectively. A few living trichinae were noted in the fourteen-hour sample, but no infections were produced on feeding. No living trichinae were found in the twenty-four and thirty-nine hour samples and no infections were produced on feeding.

Blair and Lang (1934) conducted similar tests. They performed experiments on trichinous guinea pig, rat and pork muscle. They found some active trichinae after quick freezing small pieces of infected muscle to an internal temperature of -17.8°C and maintenance at that level for a period up to 56 hours; or after exposure of meat to an internal temperature of -23.9°C for three hours; -29.4°C for five hours; -32.2°C for two hours; or -35°C for one hour. These authors reported that all larvae were killed at -35°C after two hours. They did no feeding experiments, hence, the ability of the surviving trichinae to produce infections is unknown.

Gould and Kaasa (1949) subjected portions of trichinous pork, weighing up to approximately 3¼ pounds, to temperatures of -25°C and lower, for various periods. They concluded that the following temperatures maintained for the designated periods, in the central portions of pork, were effective in killing all trichina larvae present; -27°C maintained for 36 hours; -30°C maintained for 24 hours; -33°C maintained for 10 hours; -35°C maintained for forty minutes; -37°C maintained for two minutes.

The resistance to -22°C (Expt. 4) by larvae from the guinea pig, does not agree with that observed by van Thiel (1925), and is considerably less than the resistance observed by Augustine (1933). Van Thiel's (1925) experiments on freezing thinly spread ground meat was performed in a manner that may be assumed to be comparable to the method used in the present investigation. The discrepancies between the experiments of the present author and those of Augustine (1933) may be explained by the increase in freezing time made necessary by the large samples used by the latter worker.

The low temperature in the present work was very rapidly attained and obviously the storage factor was eliminated. Augustine (1933), Blair and Lang (1934), and Gould and Kaasa (1949) worked with larger pieces of trichinous muscle, hence, the low temperatures were not as quickly produced. In addition, these authors were dealing with effects of storage at low temperatures for various periods of time and therefore a comparison of their results with those obtained by the present authors would not be entirely valid.

Experiment 6 was designed to test the effects of dehydration on the motility of *T. spiralis* larvae. Five heavily infected rats were sacrificed, the larvae recovered by artificial digestion, and transferred to normal saline. Ten active larvae were transferred with a micropipette to each of ten spot plate depressions. The normal saline was removed and each depression was filled with one of the following solutions of glycerol: 1, 2, 3, 4, 5, 10, 20, 30, 40, and 50%. Motility was checked at the end of five and ten minutes at 37.5°C under a dissectoscope. Ten larvae were maintained in normal saline at 37.5°C as controls.

The motility of the larvae is not affected by a five-minute exposure to concentrations of glycerol ranging from 1 to 50%. However, for a ten-minute exposure the motility varies inversely as the concentration. All larvae, in concentrations of 5% or less, were motile. Ninety percent of the larvae were motile at the end of ten minutes in the 10 and 20% glycerol, 70% motility in 30% glycerol, 10% motility in 40% glycerol and none was motile after a ten minute exposure in a concentration of 50% glycerol.

Experiment 7 was conducted to determine the infectivity of *T. spiralis* larvae after a five-minute subjection to 1, 2, 3, 4, 5, 10, 20, 30, 40, and 50% glycerol. Ten infected rats were sacrificed, the larvae recovered by digestion and transfered to normal saline. One thousand larvae were immersed for 5 minutes in 10 ml of each of the following glycerol solutions: 1, 2, 3, 4, 5, 10, 20, 30, 40, and 50%. One hundred larvae from a given concentration of glycerol were syringe-fed to each of five young adult male rats. Five young adult male rats were each syringe-fed one hundred untreated larvae as controls. All rats were autopsied when the infections were thirty days old and the recovered larvae counted (table 5).

Table 5 shows that the number of larvae recovered from infections with

TABLE 5.—Second generation *T. spiralis* larvae recovered from rat diaphragms 30 days after feeding larvae subjected to glycerol solutions.

Glycerol	Larvae from diaphragm number 1	2	3	4	5	Total
1%	116	166	114	114	266	776
2%	311	173	184	192	211	1071
3%	277	89	130	98	155	749
4%	508	469	285	442	219	1923
5%	208	153	160	122	185	828
10%	189	122	46	130	59	546
20%	144	342	403	188	135	1212
30%	307	298	617	489	268	1979
40%	302	179	268	254	183	1186
50%	135	364	440	300	671	1910
Controls	111	71	86	67	100	435

glycerol-treated larvae is consistently greater than the number recovered from the controls. It is suggested that glycerol may serve as a better suspension medium for trichina larvae than normal saline when feeding experimental animals by the "syringe-dilution" method.

Having observed marked lethal effects to all larvae of *T. spiralis* exposed to -32°C for one minute, experiments 8 and 8a were performed to determine: first, the protection afforded by dehydration in 50% glycerol for five minutes; second, the possible role the thawing procedure might play; and third, the comparative resistance of larvae from the guinea pig and rat in establishing infections in test animals after subjection to -28°C for one minute. *T. spiralis* larvae recovered by digestion from rat diaphragms harboring a 120-day-old infection, were dehydrated (in experiment 8) in 50% glycerol for five minutes, and subjected to -28°C for one minute. The treated larvae were immediately thawed in normal saline at 37.5°C and in air at room temperature (25°C). The motility of the experimental larvae was recorded in normal saline at 37.5°C. One hundred larvae from each group (saline- and air-thawed) were fed to each of ten young adult female rats. Five young adult female rats were each fed one hundred untreated larvae as controls. All rats were sacrificed thirty days after infection, the diaphragms digested and the recovered larvae counted.

Experiment 8a was conducted to test the resistance of *T. spiralis* larvae from the guinea pig host when treated as above. The material and methods are the same as in experiment 8 except that the experimental material was from guinea pigs.

One hundred percent of the larvae from the rat and 92% of those from the guinea pig were motile when thawed immediately in normal saline at 37.5°C. Ninety-six percent of the larvae from the rat and 88% of those from the guinea pig exhibited motility when thawed in air at room temperature (25°C). It is evident that the thawing procedure, i.e., rapid thawing in normal saline (37.5°C) in conjunction with dehydration in glycerol increases the motility of the larvae, for in experiment 5, only 51% of the larvae were motile when rapidly thawed in normal saline. Experiments 8 and 8a again demonstrate that motility is no criterion of infectivity for none of the experimental larvae produced infections in test animals.

The total number of larvae recovered from the diaphragms of five control rats fed larvae from rat diaphragm was 1,117; (av. 223 per diaphragm). The total number recovered from the diaphragms of five control rats fed larvae from guinea-pig diaphragm was 406; (av. 81 per diaphragm).

The remaining experiments were conducted in an attempt to utilize the vitrification principle (Luyet, 1937) with *T. spiralis* larvae. According to Thoennes (1940)

"The principle of vitrification is based on the fact that the formation of ice in aqueous colloids and solutions is possible only within a limited range of temperatures, between 0°C and a few tens of degrees below zero. At lower temperatures the viscosity is so high that the water molecules cannot move with sufficient freedom to become orientated in a crystalline pattern. The material then solidifies in the vitreous, amorphous state. Vitrification consists, therefore, in cooling a liquid rapidly enough to bring it below the zone of crystallization temperatures before it has time to crystallize. The vitreous material must also be warmed rapidly to escape the danger of crystallization during the second passage across the crystallization temperatures."

Luyet and Gehenio (1938) state

"The most important factors to be considered in a study of the temperatures at which animals or plants, organs, tissues, cells, or protoplasm die, are the following: 1. The species or type of material studied; 2. The external temperature to which the material has been subjected; 3. The time of action of this temperature; 4. The temperature within the dying material; 5. The time of action of this latter temperature; 6. The rate of cooling and, if the material was thawed, the rate of warming; 7. The presence or absence of ice in the tissue, in the cells or in the protoplasm; 8. The state and the conditions of the material, before and during cooling, such as, its acclimatization to low temperatures, its water content, its thermic insulation, etc."

Luyet and Hartung (1941) reported that *Anguillula aceti* solidified in liquid air during a one-minute exposure, resumed activity upon being rewarmed (water at 30°C) provided that the cooling and the rewarming were extremely rapid. When the animals had been subjected to partial dehydration by a five-to-ten-minute immersion in a 30% solution of ethylene glycol[9], the percentage of survivors was increased quite considerably. It is interesting to note that when the worms in these experiments were allowed to warm slowly for 15 seconds at room temperature before being immersed in the water, none of them survived.

In 1925 van Thiel placed small pieces of trichinous guinea pig muscle in small gauze bags and submerged them in liquid air for a period sufficient to attain the temperature of the liquid air (-192°C). He removed the meat and fed part of it to a rat or guinea pig. Another portion was digested and the larvae were examined for motility. Van Thiel stated, "I did therefore succeed neither to infect the rat or guinea pig nor see clearly living larvae". Only one among thousands of larvae that he observed showed slight motion.

After an unsuccessful attempt in the present work to revive normal (water content) *T. spiralis* larvae after solidification in liquid nitrogen (-196°C), the possibility of partial dehydration in glycerol was explored.

In experiments 9, 9a, 10, and 10a, the procedure was identical with that used in experiments 8 and 8a with the following exceptions: in experiments 9 and 9a the larvae were subjected to -78.5°C. The temperature used in experiments 10 and 10a was -196°C.

In experiments 9 and 9a, 62% of the larvae from the rat host and 25% of those from the guinea pig exhibited slight motility when thawed rapidly in normal saline at 37.5°C. None of the larvae from the guinea pig and only 1% of those from the rat was motile when thawed in air at room temperature (25°C).

None of the larvae in these two experiments produced infections when fed to rats. The greater percentage motility shown by the larvae from the rat, when thawed in normal saline again indicates that *T. spiralis* larvae from this host are more resistant to cold than those from the guinea pig.

In experiments 10 and 10a, *T. spiralis* larvae were dehydrated in 50% glycerol for five minutes and subjected to -196°C during a one-minute exposure with the hope that vitrification would be accomplished. Seventeen percent of the larvae from the rat and 7% of those from the guinea pig, when rapidly thawed in normal saline (37.5°C) appeared normal but were

[9] Glycerine was used in the present work because it is less toxic than ethylene glycol.

non-motile. All larvae from the rat and guinea pig, when slowly thawed, were non-motile and exhibited the question-mark shape and translucent granular protoplasm—phenomena considered characteristic of dead larvae by previous workers. None of the larvae in experiments 10 or 10a produced an infection when fed to rats.

The failure of larvae to survive and produce infections after solidification at low temperatures indicates that damage may be due to incomplete vitrification, i.e., to the formation of ice crystals in the parasites.

Experiment 11 was designed to test the effect of storage in normal saline, at low temperature on *T. spiralis* larvae liberated by artificial digestion. One thousand larvae were transferred to normal saline and stored in a refrigerator at 3°C. Thirty days later these larvae were removed from the refrigerator and 75% of them were observed to be motile in normal saline at 37.5°C. One hundred of these larvae were fed to each of five young adult male rats. These rats were autopsied when the infections were thirty days old, the diaphragms digested and examined but no larvae were recovered. Therefore, it is concluded from this experiment that a thirty-day exposure to 3°C is lethal to excysted *T. spiralis* larvae stored in normal saline. Levin (1940) succeeded in producing infections in test animals by feeding larvae that had been cultured in Tyrode's solution at 5°C after periods up to four months.

SUMMARY

The trichinoscope is 74.28% effective for cysts in 40-day-old, and 81.84% for 140-day-old, *Trichinella spiralis* infections.

Exposure to rapidly attained -16°C for two minutes followed by thawing immediately in saline (0.85% NaCl) (37°C), artificial digestive fluid (37°C), or in air at room temperature (22°C) has no appreciable effect on the motility of *T. spiralis* larvae. Greater infectivity was obtained with the saline-thawed larvae.

Exposure to rapidly attained -22°C for one minute is 100% lethal to larvae from guinea pig diaphragms but not to larvae from rat diaphragms although those from the former host exhibited a greater percentage of motility.

Experiments indicate that larvae from rats are more resistent to low temperatures than those from guinea pigs and that the rat is more susceptible to *T. spiralis* infections than is the guinea pig.

A one-minute exposure to -32°C is lethal to *T. spiralis* larvae from rats, although some exhibited motility after exposure.

A five-minute exposure to glycerol concentrations of 1, 2, 3, 4, 5, 10, 20, 30, 40, and 50% does not affect the motility or infectivity of *T. spiralis* larvae. After a ten-minute exposure 90% of the larvae were motile in 10 and 20% glycerol, 70% in 30% glycerol, 10% in 40% glycerol, and none after a ten minute exposure to 50% glycerol. Experiments suggest that glycerol may serve as a better suspension medium than saline when infecting experimental animals.

Subjection of *T. spiralis* larvae to a 50% solution of glycerol increases the motility of specimens thawed in saline (0.85% NaCl) at 37°C.

A one-minute exposure to -28, -78.5, and -196°C, in conjunction with

dehydration in 50% glycerol (for five minutes) is lethal to *T. spiralis* larvae from guinea pig and rat hosts regardless of thawing procedures.

Exposure to 3°C in saline (0.85 NaCl) for a period of 30 days is lethal to excysted *T. spiralis* larvae.

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Environmental Changes in a Polluted Stream During Winter

Arden R. Gaufin[1] and Clarence M. Tarzwell

Department of Health Education, and Welfare, U. S. Public Health Service
Robert A. Taft Sanitary Engineering Center, Cincinnati, Ohio

Year round studies of environmental conditions in Lytle Creek, a stream polluted with organic wastes, were initiated late in 1949, by the Biology Section of the Public Health Service's Environmental Health Center.[2] Lytle Creek is a tributary of the Little Miami River which enters the Ohio River at Cincinnati. It is about 11 miles long, and has an average width and depth of 15 feet and 1 foot respectively, during normal summer flows. Widths range from 3 to 35 feet and depths from a few inches to a maximum of 6 feet. Surface runoff comprises the major portion of the natural stream flow. During the summer months the stream has only one functional tributary below the outfall from the primary sewage treatment plant of the city of Wilmington which contributes 80 to 90 percent of the total stream flow. This large amount of organic waste quickly blots out normal stream conditions in the summer and a definite septic zone is established below the sewage outfall. However, all well recognized pollutional zones are established and the stream returns to essentially clean water conditions before it joins Todds Fork of the Little Miami River.

The aims of the Lytle Creek Study were to relate environmental conditions in various portions of the stream to the qualitative and quantitative composition of the aquatic population found in these sections; to observe seasonal changes in the fauna and the environment; and to collect other related data essential for the correlation of past ecological conditions with the composition and abundance of the aquatic fauna. The Lytle Creek investigation is one phase of an overall study designed to develop a biological method which can be used throughout most of the year and in most streams for indicating the pollutional conditions due to organic wastes which have prevailed over a considerable period in the past. Such a method would be desirable in reconnaissance surveys for indicating the severity and extent of organic pollution and the degree of stream recovery.

Ecological conditions and the composition of the fauna of Lytle Creek during spring and summer have been described by Gaufin and Tarzwell (1952). Fall and winter conditions have also been studied during the past two years. These investigations have followed the movement of ecological or pollutional zones in the stream with the seasons and with changes in flow.

Under summer conditions the stream has only one functional tributary below the source of pollution. During the winter months, however, several tributaries support a varied and abundant fauna which is contributed to the main stream during flash floods.

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[1] Present address: University of Utah.

[2] Now the Robert A. Taft Sanitary Engineering Center.

PROCEDURES

The studies which have been carried out in Lytle Creek during the past two years have been made under diverse seasonal and climatic conditions. During this period special attention has been given to ecological variations accompanying seasonal changes. Seven stations judged to be representative of the various zones or sections of zones, were selected for monthly sampling. These stations were designated by their distance in miles upstream from the

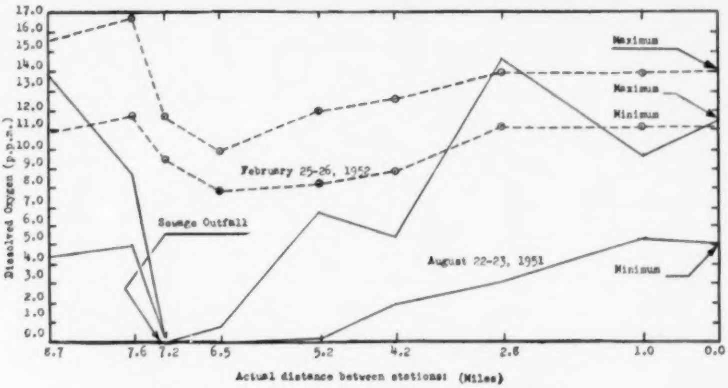

Fig. 1.—Range in dissolved oxygen, Lytle Creek

mouth as shown in fig. 1. Monthly water samples were taken at these stations for the determination of dissolved oxygen, pH, CO_2, methyl orange, and phenolphthalein alkalinity, and temperature. Diurnal and seasonal variations in physical and chemical conditions were determined by taking hourly samples at each of the stations for a 24-hour period during each season. Continuous flow records were obtained by means of a sharp crested, rectangular contracted weir and continuous float level recorder placed in the stream about 3 miles above its mouth.

Quantitative bottom samples were taken at monthly intervals at each station in pools, runs, and riffles. A Surber square foot sampler was used for taking samples from riffle areas, while a Peterson or Ekman dredge was used in other areas. Marginal samples were also taken from all sections of the stream by means of a special surface sampler, and a Needham handscreen sampler was often used in qualitative reconnaissance studies.

Biological, physical, and chemical data collected during the first year of the study showed a striking difference between summer and winter in the ecological conditions and faunal associations in the various zones of the stream. In order to gain a better idea of these differences an intensive qualitative and quantitative survey of the bottom and surface fauna of the entire stream was made during the period of May 1951 through February 1952.

During periods of high and rapid flows which are characteristic of the winter months and during which there is an abundance of dissolved oxygen throughout the stream, special attention was devoted to determining whether

clean water organisms could survive after drifting into the stream section which had been septic in summer. The fate of pollutional forms which were carried downstream was also carefully noted. Effects of seasonal changes were correlated with the life histories and habits of the organisms concerned.

RESULTS

Physical and chemical conditions.—During the last two winter seasons minimal flows in Lytle Creek have been in excess of 6 cubic feet per second (cfs) with frequent floods of 40 cfs or more. During these periods of high water the time of flow from the sewage plant to the mouth of the stream was generally less than 36 hours. Scouring floods have been frequent during the winter season. By contrast, in late summer and fall, stream flows at the weir averaged 1 cfs and the time of flow from the sewage plant to the mouth of the stream was 7 to 8 days.

A comparison of the oxygen concentrations in the stream under summer and winter conditions is given in fig. 1. It will be noted that, during the late summer, septic conditions exist in the stream from the sewage outfall to a point two miles downstream. The two miles of stream just below this section represent a zone of recovery, and the remaining two miles to the mouth represent clean water conditions. Under winter conditions, oxygen concentrations have been well in excess of the minimal requirements of most if not all aquatic organisms. The lowest oxygen value recorded during the winter of 1951-52 was 7.8 ppm on February 25, 1952, at midnight at a point 0.7 miles below the sewage outfall. This represented 57% of saturation. Water temperatures range from 32° to 50°F during the three winter months.

Biological conditions.—Reconnaissance surveys conducted during October 1951, revealed ecologic conditions quite similar to those encountered during the late summer. Well defined zones of pollution still existed in the stream and the composition of the fauna present was not much different from that reported in the stream for August 1951 (Gaufin and Tarzwell 1952). By the middle of November, however, the biota indicated that the effects of pollution were moving downstream. By January the carpet of *Sphaerotilus*, bacteria, and protozoa characteristic of the summer septic zone extended three miles downstream to the formerly clean water zone. The lower two miles of the stream exhibited pollutional fauna intermixed with clean water forms.

Many of the clean water organisms found in the lower part of the stream during the summer disappeared during the winter. It is assumed that some of these as the Coleoptera and Odonata burrowed deeper into the stream bed or banks and were not taken by the sampling methods used. Other forms had emerged and were replaced by a winter fauna. Many were washed downstream or destroyed by the molar action of floods. The continued existence of those that remained was imperiled by a slimy growth of *Sphaerotilus* which blanketed the bottom. That this growth offered formidable competition to the aquatic insects was evidenced by the fact that nymphs of the mayfly, *Stenonema femoratum*, a clean water form, were found on several occasions so densely covered with *Sphaerotilus* that their continued existence seemed an impossibility (fig.2).

Many clean water forms were washed by floods from the upper section of the stream or from winter time tributaries into the unfavorable habitat

Fig. 2.—Mayfly, from zone of recovery covered with *Sphaerotilus*, showing effects of pollutional blanket on macro-invertebrates.

offered by the stream below the sewage plant. Some of these forms were even encountered in leaf drifts directly below the sewage outfall during such high flows. Their existence was short-lived, however, as no clean water forms could be found alive in the formerly septic zone after the flow had become more stabilized.

During January and February 1952, pollutional tolerant tubificid worms and *Chironomus decorus* larvae, the most abundant members of the summer septic and recovery zones, were found in large numbers in riffles extending even to the mouth of the stream. As many as 3,000 tubificids per square foot were collected in a formerly clean water area. At Station 2.8, a clean water station in summer, these forms had largely replaced the clean water fauna. In some instances, however, many of the worms showed incomplete adaptation to their new habitat, as indicated by their beaded condition.

A comparison of the number of species present and the species composition of the population in the stream under autumn and winter conditions offered further evidence of ecological change. During October 1951, 43 species of macro-invertebrates were taken from the clean water section above the sewage plant, 8 different forms from the septic zone, 9 from the recovery zone, and 70 from the lower clean water section. During January and February 1952, 52 species were collected from the first mentioned section, 18 from the summer season septic zone, 5 from the recovery zone, and only 25 from the lower section of the stream. Among the 18 species collected during the winter from the summer septic zone, 10 were drift forms directly traceable to nearby tributaries. The marked reduction in the number of species in

the lower section was largely due to the extension of a pollutional blanket over much of the stream bottom. The species composition of the populations found at the different stations in the stream during the autumn and winter surveys are given in table 1.

A comparison of the number of species present and the species composition of the fauna in the different pollutional zones of the stream during the autumn and winter not only offers evidence of seasonal ecological changes but also reveals the lasting effects of pollution. In the two mile section of stream below the sewage outfall only one-fifth as many species of macroinvertebrates occurred during both seasons as were found in the upper two miles of the stream. This was due not only to the eliminating effects of oxygen depletion during periods of high temperature and low flow but also to changes in the nature of the stream bottom, and to different faunal associations. Reference to table 1 and fig. 3 will reveal a striking reduction

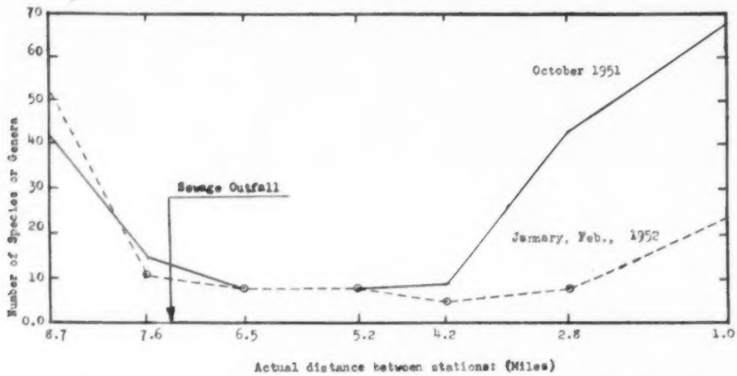

Fig. 3.—Macro-invertebrate distribution, Lytle Creek, fall and winter conditions.

in the number of different species in the mile section above the sewage plant that cannot be attributed to the effects of the sewage effluent. This change in species number and composition of the population was brought about by the introduction into the stream during periods of heavy runoff of drainage from the streets of Wilmington, and raw sewage from a break in the sewage line siphon where it passes under Lytle Creek. Although these wastes were insufficient to produce severe and lasting periods of oxygen depletion such as occurred below the sewage plant, they were still present in sufficient quantity and often enough to stimulate the growth of *Sphaerotilus*, tubificids, and pollution tolerant forms that crowded out or destroyed a balanced clean water fauna. In the portion of this section immediately below the point of entry of the street drainage ditch, a mayfly, *Stenonema femoratum*, and numerous tubificid worms were found associated in riffles even during periods of low flow. As the breakdown of oil, street, and other wastes proceeded, changes in the stream bottom and oxygen content resulted in the elimination of mayflies from the fauna. In the lower half of this section no mayflies, stoneflies, or caddis flies were found during October and only drift forms were taken during the winter.

Analyses of the prefered habitats, habits, and life histories of some of

TABLE 1.—Distribution of Invertebrates in Lytle Creek
October and January-February 1951-52

Organisms	October 1951 Stations[1]							January-February 1952 Stations						
	8.7	7.6	6.5	5.2	4.2	2.8	1.0	8.7	7.6	6.5	5.2	4.2	2.8	1.0
DIPTERA														
Polypedilum illinoense						C	C	C	C	F				
Microtendipes pedellus								F						
Chironomus decorus	F[2]			C	C	F	F	F		F	C	C	C	C
Polypedilum spp.				F		F		C						
Anatopynia dyari	F					F	F	F						
A. fastuosa	F													
Cricotopus bicinctus	F					F	F	F						
Corynoneura scutellata	F													
C. sp.	F													
Stictochironomus varius	C					F		C					F	F
Hydrobaenus obumbratus	F							C						
H. sp.								F						
H. spp.	C	F				C	F	C		F	F		F	F
Pentaneura flavifrons (?)	F	F						F						F
P. melanops	F	F								F				
P. monilis (?)	F						F	F						
Tanypus stellatus	F													
Tanytarsus nigripilis								F						
T. similatus								F						
Anopheles punctipennis	F			F			F							
Culex pipiens			F			F	F							
Eristalis bastardi			C			F				F				
Tabanus atratus	F						F			F				
Tabanus sp.						F	F	F						C
Simulium vittatum	C				F	C	C	F						
Pilaria sp.								F						
Limnophila sp.	F						C							F
Tipula abdominalis								F						
T. sp.	F	F					F							
Hemerodromia sp.							F							
Dictya sp.						F	F							
Argyra sp.											F			
COLEOPTERA														
Peltodytes G. maculatus							C							
P. lengi							C			F				
P. duodeno-punctatus							C							
P. edentulus	C						F	F						
Gyrinus lugens						C		F						
Dineutes americanus					F	C	C							
Psephenus lecontei							F							
Stenelmis crenata	C							C						
S. sexlineata	C						C	C						F
Helichus lithophilus							C							
H. basalis							F							
Agabus stagninus								F						
Hydroporus pulcher		F					F	F						
H. wickhami							F							
H. mellitus							F							
Coptotomus i. interrogatus					F									
Laccophilus maculosus		F				C	F	F						
L. fasciatus						F								
Tropisternus lateralis nimbatus						C	F							

TABLE 1.—(Continued).

Organisms	October 1951 Stations							January-February 1952 Stations						
	8.7	7.6	6.5	5.2	4.2	2.8	1.0	8.7	7.6	6.5	5.2	4.2	2.8	1.0
T. mexicanus striolatus						C								
T. natator	F	F		F			F	F		F				
Laccobius agilis	F						F							
Helochares maculicollis							F							
Enochrus pygmaeus nebulosus		F					C							
Berosus peregrinus							F							F
EPHEMEROPTERA														
Ameletus sp.							F							
Blasturus collinus									F					
B. sp.								F						
Baetis parvus	C					C	C							
Callibaetis sp.	F					F								
Caenis spp.	C						C	F						
Isonychia albomanicata							F							
Stenonema femoratum	C					C	C	C	F	F	F			F
S. tripunctatum						C	C	F						F
S. interpunctatum group							F	F						
TRICHOPTERA														
Cheumatopsyche sp.								C						
Hydropsyche bifida							F							
H. betteni	C					C	C	C						
Helicopsyche borealis							F							
Hydroptila sp.	F						F							
Pychopsyche sp.								F						
Rhyacophila lobifera								C	F				F	C
PLECOPTERA														
Acroneuria evoluta								F						
Allocapnia viviparia								N	F	F	F			F
Isoperla confusa								F						F
I. decepta								C	F					
Neophasganophora capitata							F							
NEUROPTERA														
Corydalis cornutus						F	C						F	F
Sialis sp.						F	C	F						
ODONATA														
Boyeria vinosa							F							
Dromogomphus sp.							F							
Gomphus sp.	F						F							
Anax junius						F								
Libellula lydia	F	C			F	C	C		F	F			F	F
Libellula pulchella							F							
Agrion spp.	F	C				C	C		F					
Argia spp.	F	C				C	C		F					F
Enallagma spp.		C			F	C	C		F		F		F	F
HEMIPTERA														
Belostoma sp.				F		C	F	F						
Corixidae	F					C	C				F			

TABLE 1.—(Continued).

Organisms	October 1951 Stations 8.7	7.6	6.5	5.2	4.2	2.8	1.0	January-February 1952 Stations 8.7	7.6	6.5	5.2	4.2	2.8	1.0
Gerris sp.	F					F	F							
Microvelia sp.						C	C							
Notonecta sp.						F								
Nepa sp.						F								
Ranatra sp.						F	F							
Trepobates sp.	F													
CRUSTACEA														
Asellus sp.			F			F								
Mancasellus sp.	F							C		F				F
Cambarus rusticus								C						
Gammarus sp.								C	F	F				
PLATYHELMINTHES														
Planaria sp.								C	C		C			
NEMATHELMINTHES														
Nematoda sp.							F							
Paragordius sp.											F			F
ANNELIDA														
Pristina sp.						C	C							
Stylaria sp.	F					F	F							
Dero spp.							F							
Limnodrilus sp.	F	N	N	N	N	F	F	F	C	C	N	C	C	C
Tubifex sp.		C	C	C	C				N	C	C	C	C	C
Helodrilus chloroticus								F		F				F
Eiseniella tetraedra								F	F	F	F	F		
Lumbricus sp.			F					F		F	F			F
Glossiphonia sp.						F	F	F						
MOLLUSCA														
Physa integra	F	C	F	C	C	C	F	F	F			F	F	F
Ferrissia rivularis							C							F
Musculium transversum							F							
Pisidium casertanum	F								F					
Sphaerium solidulum		C	F					C	C					
Lymnaea humilis modicella	F					F								
Total species per station	43	15	8	8	9	44	70	52	3a 18	3b 18	3c 13	5	10	25

[1] The stations are classified into zones of pollution as follows: Clean water, 8.7, 2.8, and 1.0; Septic Zone, 6.5 and 5.2; Zone of moderate pollution or recovery, 7.6 and 4.2.

[2] F=Few, occasional specimen to 2 per square yard
C=Common, 3-50 per square yard
N=Numerous, 51 or over per square yard

[3a,b,c] Includes 7, 10, and 3 drift forms respectively from clean water areas.

the organisms listed in table 1 yields rather interesting information as to their value as indicators of pollution in a stream. Diptera or fly larvae are adapted to live under a wide variety of environmental conditions but only 7 of 23 species collected during the winter period were able to survive the effects of the pollutional stream bottom blanket which moved downstream. The only

species which was widely distributed throughout the stream was *Chironomus decorus*. In October it was the most common invertebrate found in the riffles in the lower septic and the recovery zones but only an occasional specimen was found in clean water areas. During the winter as the pollutional blanket moved downstream *C. decorus*, upon being washed downward, congregated in large numbers in riffles in even the formerly clean water zone. One species of Diptera, *Culex pipiens*, which was found in large numbers in the septic zone during the summer, disappeared completely in the winter. Another, *Eristalis bastardi*, was represented by only a single specimen during the winter, that from the zone which had been septic under summer conditions.

Reference to the orders Ephemeroptera, Trichoptera, and Plecoptera reveals that all representatives of these orders were restricted to clean water areas during the October survey. Only one or two species from each group were taken during the winter from the formerly septic zones. Of these forms, *Stenonema femoratum*, a mayfly, was found to possess considerable tolerance to pollutional conditions if the dissolved oxygen supply was present in ample quantities. Nymphs of this species were found associated with *Chironomus decorus* and tubificid worms in riffles where other invertebrates had been eliminated by the pollutional blanket.

Larvae of the caddisfly, *Rhyacophila lobifera*, and nymphs of the stonefly, *Allocapnia viviparia*, were also collected from areas which showed definite signs of pollution, but only directly following heavy floods. Wherever they occurred they were present in very small numbers and were found clinging to masses of drifting leaves or debris. Neither species seemed to be able to adapt itself to the polluted conditions in the stream and disappeared when the flow became stabilized. The source of both species in all such instances was found to be the numerous intermittent tributaries which feed Lytle Creek during the winter time.

DISCUSSION

In order to utilize aquatic populations as an index in evaluating the degree, severity, and duration of pollution in a stream, it is essential to have a knowledge of the species composition and abundance of the various organisms in the population. Further, consideration must be given to the fact that pollution with organic waste is only one of several environmental factors determining the composition of aquatic populations. Other environmental factors such as the nature of the stream bed, variations in flow, severity of floods, water temperatures, location, type, and population of tributaries, and the character of the watershed are all important in determining the make-up of of aquatic populations.

Under winter conditions oxygen depletion is not a limiting factor to the distribution of aquatic invertebrates in Lytle Creek. With a decrease in water temperatures and an increase in the volume and velocity of flow, the pollutional carpet of organic and mineral matter deposited in the septic and recovery zones during low flow extends further downstream encroaching on or eliminating the former recovery and clean water zones. Bottom organisms from the clean water, recovery, and septic zones congregate together in riffles during floods making a delineation of biological zones of pollution difficult if not impossible. Tributaries, during times of flood, contribute fauna not

normally found in the main stream, thus necessitating a consideration of the source and habits of the forms collected before an adequate interpretation of the data can be made. In winter as well as in summer the mode of occurrence of the organisms in the stream must be taken into account in determining the effects of pollution. A relatively large number of pollution-tolerant forms as tubificids associated with very few clean water forms may be indicative of past floods and an extension of pollutional conditions. Inability of the clean water forms to continue to survive attests to the critical conditions imposed by organic pollution even in the presence of an ample oxygen supply. This is demonstrated by the significant reduction in the number of species in the lower clean water section of Lytle Creek during the winter of 1951-52, and by the downstream extension of bottom conditions characteristic of the septic zone (fig 3).

A knowledge of the life histories of the various groups of aquatic insects often is essential in interpreting the meaning of their distribution. The presence of such forms as *Culex pipiens* and *Eristalis bastardi* in large numbers in the septic zone during summer and their absence during cold winters should be considered as a normal phase of their developmental pattern. The disappearance of certain beetles, dragonflies, and damselflies from a polluted stream during winter should not be necessarily interpreted as indicative of more unfavorable pollutional conditions but rather as a normal response of hibernating under winter conditions. Thus, one who is acquainted with the distribution, habits, and life histories of aquatic organisms can learn considerable about the pollutional conditions in a stream even when physical chemical indications of pollution are least evident.

SUMMARY

In the summer months during periods of high temperature and low flow, the septic and recovery zones are shortened, and most of the biochemical oxygen demand is satisfied in a relatively short section of the stream, about 70% in 2 miles in Lytle Creek. During the summer, diurnal variations in dissolved oxygen are at a maximum and severe oxygen depletion occurs; the effects of pollution are most evident and the life zones are more clear cut and readily observed. The fauna occurring in the septic and recovery zones are able to exist in the absence of free oxygen, have low oxygen requirements, or have special adaptations for obtaining oxygen. With an abundance of food and an absence of competition from other forms these organisms thrive and build large and distinctive populations.

In the winter months, stream flow in Lytle Creek is greater and more rapid, metabolic activity is at a lower level; life zones become longer or lose their identity, and diurnal variations in dissolved oxygen are at a minimum, the lowest concentrations never approaching those of summer. The increased rate of flow and shorter retention time in the stream coupled with a slower rate of bacterial action serves to carry higher concentrations of organic material into the lower sections of the stream. As a result of this greater organic content, the pollutional carpet of bacteria, protozoa, and entrapped organic materials which is characteristic of the septic zone in summer, extends further downstream. When severe floods do not occur for considerable periods the pollu-

tional carpet reaches the upper end of the clean water zone of summer.

This downstream extension of the pollutional carpet in the winter of 1951-52 brought about a significant reduction in the variety of macro-invertebrates in the lower clean water section of Lytle Creek. Even though dissolved oxygen is adequate this carpet and other factors constitute a definite barrier to the establishment of clean water insects. Such forms migrating or washed into the main stream from the upper clean water zone or from tributaries did not long survive in the former septic or recovery zone of summer. In these areas they are found only in leaf drift piles after floods. However, this introduction of clean water organisms from the tributaries to the main channel of a polluted stream during high winter flows constitutes a factor which should be considered in evaluating the reliability of macro-invertebrates as indicators of stream conditions. Also during the winter months bottom organisms characteristic of the septic and recovery zones during summer may be carried to points further downstream. Riffles in the clean water area may serve to collect organisms normally found in pools or along margins in other sections of the stream. It is apparent, therefore, that some knowledge of the habits, habitats, and life histories of many macro-invertebrates is essential for their effective use as biological indicators of pollution.

Because the composition and abundance of stream populations are determined by environmental conditions which have prevailed or by extremes which have occurred during their life cycle, organisms having an annual life cycle are especially valuable as biological indicators of past environmental conditions. The absence of long life history and clean water forms is much more significant than the presence of short life history and tolerant forms. A knowledge of the habits and environmental requirements of bottom organisms enables the aquatic biologist, by means of a brief qualitative quantitative survey to gain some knowledge of past conditions, the severity and extent of pollution, and the degree of recovery.

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Bottom Fauna of a Shallow Eutrophic Lake, Lizard Lake, Pocahontas County, Iowa[1]

Leonidas B. Tebo, Jr.[2]
Iowa State College, Ames

The State of Iowa is carrying on a dredging program in an attempt to rehabilitate many of the lakes in the northern part of the state. Most of these lakes are of glacial origin and are in the later stages of succession. They are of little value for boating and swimming because of the shallow depth and heavy growths of aquatic vegetation. The fish populations in many of them cannot be maintained because of their vulnerability to winter kill. By means of dredging, the life of these lakes is prolonged and sufficient depth is provided to support a fish population throughout the year. The increased depth and decrease in aquatic vegetation makes them more suitable as recreational areas. Conditions in these lakes are radically altered as a result of dredging and it is desirable to know what effect this has on the biological productivity. The bottom organisms are directly affected by dredging and it is believed that they can be used as an index to measure any changes in the productivity of these lakes.

Lizard Lake was selected for a bottom fauna study because it will be dredged in the near future. This paper deals with the data gathered from Lizard Lake in the summer of 1951, before dredging of the lake, and will provide a basis for comparing the productivity in terms of bottom fauna after the lake has been dredged. Several sampling techniques were used to determine which would give the best results in different types of habitat.

Lizard Lake, located in Lake Township, Pocahontas County, Iowa, has a surface area of approximately 268 acres (fig. 1). The maximum depth found in July, 1951, was 5 feet and much of the lake was between 4 and 5 feet deep. There are no docks or cottages around the lake and the surrounding land is devoted entirely to agriculture. Most of the land in the immediate vicinity of the shoreline is wooded or open pasture. The main inlet flowing into the shallow bay at the southwest corner of the lake provided water throughout the summer of 1951. The outlet is at the north end of the lake and drains into the west fork of Lizard Creek and thence to the west fork of the Des Moines River.

Chemical and temperature readings indicated very little stratification from top to bottom during most of the summer. By the middle of August most of the surface of the central part of the lake was covered with a dense growth of sago pondweed, *Potomogeton pectinatus*. Methyl orange alkalinity ranged from 180 to 230 parts per million during the summer. Turbidity was almost entirely due to silt suspended in the water after periods of high wind. On calm days the Ekman sampler could be seen on the bottom at a depth of 4 feet.

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[1] From Project 42 of Iowa Cooperative Fisheries Research Unit, sponsored by the Iowa State Conservation Commission and the Industrial Science Research Institute of Iowa State College.

[2] Now Aquatic Biologist, North Carolina Wildlife Resources Commission, Coweeta Hydrologic Laboratory, R. No. 1, Dillard, Ga.

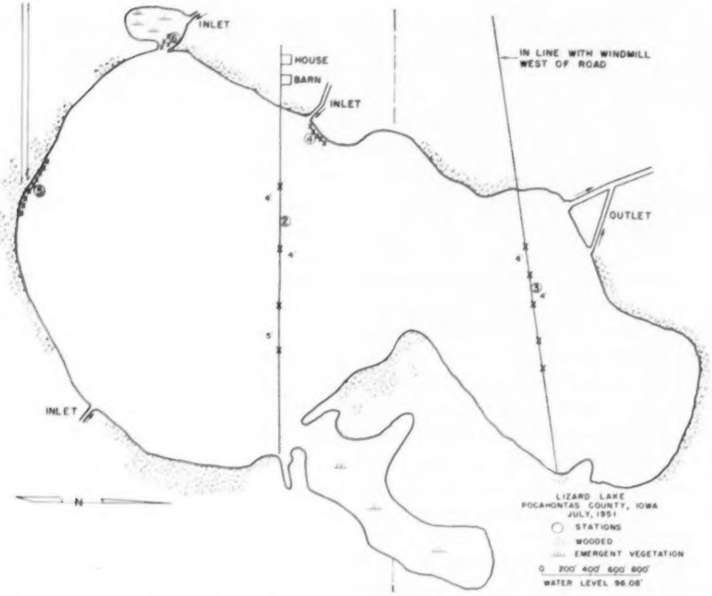

FIG. 1.—Map of Lizard Lake, Pocahontas County, Iowa, showing sampling stations.

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DESCRIPTION OF STATIONS

Six sampling stations were established but station 1 was abandoned early in the study and is not included in the present report. The bottom soils in this paper are designated according to the classification outlined by Roelofs (1944). The higher plants were identified using Fassett (1940) and by comparison with specimens in the Iowa State College herbarium. The algae were identified using Prescott (1951).

Station 2 is a line transect located in the south central part of the lake (fig. 1). The bottom is pulpy peat and the water depth varies from 4 to 5 feet. *Potomogeton pectinatus* was the only plant collected at station 2 and by the middle of August it had formed dense mats on the surface of the entire central portion of the lake.

Station 3 is a line transect located in the north central part of the lake (fig.

1). The bottom is pulpy peat and the average depth of the water is approximately 4 feet. *Potomogeton pectinatus* was also abundant at this station and a filamentous algae, *Rhizoclonium hookeri*, was found entangled among the submerged stems.

Station 4 is located along the wooded south shore (fig. 1). All samples at this station were taken at a water depth of 12 to 18 inches. The bottom is composed of sand and gravel with small amounts of detritus. Station 4 was shaded at all times by the trees along the steep bank and no higher plants were present. A filamentous algae, *Ulothrix* sp. was taken in some of the samples but was not abundant.

Station 5 is located along the west shoreline just north of a ditch flowing into the lake (fig. 1). All samples were taken at a depth of 12 to 18 inches. The bottom is composed of fine sand and clay with small amounts of detritus. Heavy growths of filamentous algae were noted at this station and may possibly be due to nutrients received from the small ditch which flows across an open pasture before reaching the lake. Specimens of algae taken in the bottom samples were: *Cladophora crispata, C. fracta, Rhizoclonium fontanum* and *Ulothrix* sp. There were sparse growths of *Scirpus validus* and *Eleocharis* sp. at station 5 in July but this vegetation almost entirely disappeared later in the summer.

Station 6 is located in a heavily vegetated, shallow bay at the southwest corner of the lake (fig. 1). All samples were taken at a water depth of 18 to 24 inches. The bottom is composed of fibrous and pulpy peat with small amounts of fine sand. *Potomogeton foliosus* and *Najas flexilis* were the dominant submerged and floating-leaved species at station 6 and formed mats in August and September. The following additional plants were collected: *Scirpus validus, S. fluviatilis, Utricularia vulgaris, Alisma subcordatum, Sagittaria latifolia, S.* sp., *Potomogeton pectinatus, Polygonum coccineum, Sium suave, Lemna minor, L. trisulca,* and *Spirodela polyrhiza.*

SAMPLING METHODS

Four types of collecting apparatus were used in sampling the bottom fauna of Lizard Lake. A standard Ekman dredge, 6 inches square, was used at the deeper water stations. Petersen, Dendy and stovepipe samplers were used for sampling at depths of 18 to 24 inches along the shore (Welch, 1948). For the stovepipe sampler a 24 inch section of stovepipe having a diameter of 7 inches was used. The complete stovepipe sample was collected by removing the top layers of soil by hand, and mixing the remaining bottom materials with the water in the stovepipe. The mixture of bottom materials and water was removed from the stovepipe with a small hand dipper.

The Dendy, stovepipe and Petersen samples collected at station 4 in September were compared by the method of analysis of variance (table 1). The calculated F value is so low that there is apparently no appreciable difference in the estimates of bottom fauna taken by the three different samplers. Appreciable differences may exist between the methods but because of the excessive variability due to uneven distribution of the organisms these differences remained undetected.

On the assumption that the variance remains constant the minimum

number of samples required to keep the standard error within ten percent of the mean was determined by the formula $N = \frac{100\ s^2}{Y^2}$ (table 2).[3] Since the assumption that the variance remains constant is probably not satisfied the formula only gives a rough approximation of the actual number of samples required. Nevertheless the values obtained are useful for comparative purposes.

Time limitations would of course prevent taking such large series of samples but the large values give us an indication of the tremendous variability between samples. Because of the amount of variation, any quantitative generalizations based on a few bottom samples may be subject to a great deal of error. If a standard error with 20 percent of the mean were accepted the number of samples needed would be only one-fourth of those indicated in table 2.

The large value for the Ekman sampler indicates that the bottom in the deeper parts of Lizard Lake is not as homogeneous as was assumed when the stations were set up.

The value of 1,658 samples for the Dendy sampler is out of line even when the large number of samples which can be taken with this sampler is considered. The Dendy samples at station 6 also showed a large range in values (5,793 for 10 samples taken in September). The large range in values brings out a disadvantage of the Dendy sampler which in the author's opinion makes it undesirable for use on a bottom of coarse materials. Because of the uneven nature of the bottom at stations 4 and 6 the distribution of the organisms is not homogeneous but they are scattered in small concentration pockets. The small size of the Dendy makes it possible to hit in and out of these pockets with the result that many of the samples give exaggerated values that are either very high or very low.

All samples were collected during the periods July 11-23, August 13-21,

TABLE 1.—Analysis of variance for sampling methods on the basis of milligrams dry weight per square meter at station 4 in September, 1951, Lizard Lake, Iowa

Source of Variation	Degrees of Freedom	Sum of Square	Mean Square
Between methods	2	268,363	134,182
Within methods	14	14,010,781	1,000,770
	$F = 0.13408$		

TABLE 2.—Number of samples required to keep the standard error within 10 percent of the mean. Based on dry weights of samples taken at stations 2 and 4 in September, 1951.

Sampling Method	N
Dendy	1,658
Stovepipe	54
Petersen	19
Ekman	486

[3] Where s = standard deviation and Y = mean.

September 6-10 and October 6, 1951. The bottom materials were washed through 40 mesh screen, placed in jars and preserved in 4 percent formaldehyde. Each sample was labelled and kept separate so that the data could be subjected to statistical analysis. The organisms and plant detritus were separated from the sand in the shore samples by placing the sample in a large tub with water, swirling it vigorously, repeatedly pouring off the suspension of organisms and debris. Slightly greater than 98 percent separation of organisms from the sand was accomplished using this method. The sand was divided into aliquot portions and one-fourth of the total was saved.

For dry weight determination the organisms in each major taxonomic group were divided into size classes and large numbers of each size class were dried to a constant weight in an electric oven at 70°C. The mean of three samples was used to obtain a conversion factor for converting the number of organisms in each sample to the dry weight. The shells of all molluscs were removed with dilute hydrochloric acid before weighing.

QUALITATIVE ANALYSIS OF THE BOTTOM FAUNA

Most of the aquatic invertebrates collected in this study were identified by the author with the use of existing keys. The following authors were followed in the identification of the various specimens collected: Molluca: Eddy and Hodson, 1950; Crustacea: Ward and Whipple, 1918, Pratt, 1935; Ephemeroptera: Needham, Traver and Hsu, 1935; Odonata: Garman, 1927, Needham and Heywood, 1929; Trichoptera: Ross, 1944; Coleoptera: Needham and Needham, 1941; Tendipedidae: Johannsen, 1937a, 1937b, Hauber, 1945a, 1945b, 1947. The Ephemeroptera and Zygoptera were determined from specimens reared to the adult stage. With the exception of the Hemiptera all other aquatic insects were determined from immature specimens. The identifications of the Ephemeroptera were verified by Mr. Eugene W. Hamilton of the University of Nebraska. Mr. Richard C. Froeschner of Iowa State College identified all of the aquatic Hemiptera collected. Particular attention was devoted to the midge family Tendipedidae which appeared to be the most abundant and widespread group of bottom invertebrates in Lizard Lake. The nomenclature followed for the Tendipedidae is that given by Johannsen and Townes (1952).

TURBELLARIA

Several flatworms were collected along the shore on sand and gravel bottom and on sand and clay bottom at a water depth of 12-18 inches.

NEMATODA

Free living nematodes were most abundant in the samples collected on sand and gravel bottom at a water depth of 12-18 inches. A few specimens were collected in shallow water from the sand and clay bottom at station 5 and from the pulpy peat bottom at the deep water stations.

OLIGOCHAETA

Oligochaetes were common at both deep and shallow water stations in Lizard Lake. They were much more abundant at the shallow water stations and the greatest numbers were found in samples taken on a fibrous and pulpy

peat bottom in the heavily vegetated bay at station 6. Although common at the deep water stations during August, September and October, no oligochaetes were found in samples from deep water during July.

HIRUDINEA

No leeches were collected in deep water. They were most abundant in samples collected on sand and gravel, and sand and clay bottom in shallow water. Most of the specimens collected on the sand and gravel bottom at station 5 were attached to small rocks.

The leeches were not included in the quantitative data because extreme variability in size made it impossible to divide them into size groups for weight determination. Because of their relatively large size and low utilization by fish they would tend to confuse the quantitative data from a standpoint of food production. A number of workers have found that fish seldom utilize leeches as food (Bennett, Thompson and Parr, 1940; Leonard, 1940; Howell, 1942; Ball, 1948; Patriarche and Ball, 1949).

MOLLUSCA

Helisoma sp.—Two species of *Helisoma* were collected; one having a shell with rounded whorls and one having whorls with acute shoulders. These snails were most abundant in samples taken in shallow water and they were common in smaller numbers at the deep water stations. Samples taken at station 6 in the heavily vegetated bay contained the largest numbers of *Helisoma* of both species. The species with rounded whorls was most abundant in deep water and the species with acute shoulders was rarely collected in deep water.

Physa sp.—*Physa* was rarely taken in the deep water samples and its distribution was very similar to that of the species of *Helisoma* with acute shoulders.

Anodonta sp.—One specimen collected on the sand and gravel bottom at station 4 in July.

CRUSTACEA

Estheria mexicana Claus.—These shell shrimp were common on the sand and gravel bottom at station 4 and were not found at any other station. Most of the specimens were collected by seining along shore. Only one specimen was collected in the bottom samples.

Hyalella knickerbockeri (Bate).—This little fresh water amphipod was abundant at all the shallow water stations. It was commonly collected where there were growths of filamentous algae and the greatest numbers were found on the heavy growths of filamentous algae at station 5. It was also commonly collected in small numbers at the deep water stations.

Cambarus sp.—One crayfish was collected in a bottom sample at station 4 in July.

HEXAPODA

EPHEMEROPTERA

Mayflies of the family Baetidae were common at all the shallow water stations. Only four specimens were collected in deep water samples. *Caenis forcipata* McDunnough.—Most abundant of the mayflies in the bottom samples from Lizard Lake. Very common at all the shallow water stations during

all sampling periods, with the greatest numbers being collected on the sand and gravel bottom at station 4. *Callibaetis* sp.—Rarely taken in bottom samples. Two specimens collected at station 6 and one at station 5. *Baetis* sp.—Rarely taken in bottom samples. One specimen collected at station 3 and one at station 5.

ZYGOPTERA

Damselflies of the family Coenagrionidae were common in bottom samples collected at both deep and shallow water stations in September and October. Three species were identified from reared specimens: *Enallagma civile* (Hagen), *E. carunculatum* (Morse), and *Ischnura verticalis* (Say). *I. verticalis* and *E. civile* were the most common species taken in bottom samples.

ANISOPTERA

Anax junius (Drury).—Two specimens found in bottom samples taken in the heavily vegetated bay at station 6 in August.

Libellula pulchella (Garman).—Two specimens collected at station 6 in October.

HEMIPTERA

Although the aquatic Hemiptera are not true benthic forms they were quite common in bottom samples from the sand and gravel bottom at station 4 and from the sand and clay bottom at station 5. They were rarely taken at the other stations in Lizard Lake. The following genera and species were identified by Mr. Froeschner: *Corisella tarsalis* (Fieber).—One specimen from station 5 and one from station 4 in July and August respectively. *Trichocorixa kanza* Sailer.—This was the most abundant species of Corixidae collected in bottom samples from Lizard Lake during August and September. *Sigara alternata* (Say).—One specimen collected at station 4 in September. *Palmocorixa buenoi* Abbott.—Several specimens collected at stations 4 and 5. *Notonecta undulata* Say.—Rare in bottom samples. One nymph and one adult collected at station 6 in September. *Buenoa* sp.—Rare in bottom samples. One nymph collected at station 4 in July.

TRICHOPTERA

A few caddis flies were collected in deep water samples but they were most abundant in the shallow water samples.

Leptoceridae: *Oecetis sp. a* of Ross (1944).—Common on sand and gravel bottom at station 4 and on sand and clay bottom at station 5 dwelling in a case constructed of fine particles of sand. *O. inconspicua* (Walker).—Two specimens were collected on sand and gravel bottom at station 4. *O.* sp.—This undetermined species was very abundant in samples taken at stations 4 and 6.

Hydroptilidae: *Agraylea multipunctata* Curtis.—Common at stations 5 and 6. Several specimens were found attached to submerged stems of *Potomogeton pectinatus* in deeper water samples at stations 2 and 3. The fibrous case which was found attached to submerged stems and roots of aquatic plants is pictured by Betten (1934, p. 501).

COLEOPTERA

Aquatic beetle larvae were not common in the bottom samples from Lizard Lake. No adult beetles were taken in the bottom samples. Sixteen specimens representing the following families and genera were collected.

Gyrinidae: *Dineutes* sp.—Nine specimens collected from sand and gravel bottom at station 4 in July and August. Adult *Dineutes assimilis* and *Gyrinus* spp. were common on the surface of the lake in September.

Haliplidae: *Peltodytes* sp.—Four specimens found in samples collected from the heavily vegetated bay at station 6 during July and August. *Haliplus* sp.—One specimen from station 4 and one from station 6 both collected in September.

Dytiscidae: *Laccophilus* sp.—One specimen collected at station 5 in July.

DIPTERA

With the exception of an undetermined puparium which was very abundant at station 4 the only dipterous larvae collected in the bottom samples belonged to the midge family Tendipedidae. Nineteen genera and species representing three subfamilies were identified.

Pelopiinae (= Tanypodinae): *Pentaneura mallochi* (Walley).—Rare in bottom samples. Four specimens collected in September; two from sand and clay bottom and two from sand and gravel bottom. *Pelopia stellata* Coquillett. —One specimen collected in deeper water in August. *Tanypus sp. b.* of Johannsen (1937a).—Common in deeper water at station 3 in July. *Procladius* sp.—Very abundant and most characteristic tendipedid at the deep water stations throughout the sampling period. A few specimens were collected at each of the shallow water stations. All specimens appeared to be of the same species on the basis of larval characters. *Coelotanypus* sp.—Common at deeper water stations during August, September, and October sampling periods. None collected in shallow water.

Hydrobaeninae (= Orthocladiinae): *Hydrobaenus* (*Trichocladius*) *senex* Johannsen.—Rare in bottom samples. Six specimens collected in shallow water at stations 5 and 6. *Cricotopus* sp.—Rare in bottom samples. Several specimens collected in deeper water at station 3 and in shallow water at stations 4 and 6.

Tendipedinae: *Harnischia* (*Harnischia*) *abortiva* (Malloch).—Rare in bottom samples. Collected at both deep water stations and from the fibrous and pulpy peat bottom at station 6. *Tendipes* (*Limnochironomus*) *modestus* (Say).—Rare in bottom samples. One specimen identified from a bottom sample collected at station 6 in July. *T.* (*Tendipes*) *tentans* (Fabricius).—Very abundant in samples collected on pulpy peat bottom in deeper water and in samples collected from the fibrous and pulpy peat bottom at station 6. None were collected at stations 4 and 5 in shallow water. This is the largest tendipedid in Lizard Lake and cannot be separated from *T. plumosus* on the basis of larval characters. *T. tentans* should be considered as tentatively occurring in Lizard Lake until rearing experiments have been conducted. *T. plumosus* is considered a profundal form but has been collected in water 3-6 feet in depth (Johannsen, 1937b). *T.* (*T.*) *decorus* (Johannsen).—Tentatively identified as *T. decorus* on the basis of size, otherwise inseparable from *T. tentans* and *T. plumosus* on basis of larval characters. Common at stations 6 in August and September. *T.* (*Limnochironomus*) sp. At least two species of the subgenus *Limnochironomus* occur in Lizard Lake. The very abundant tendipedid fauna at station 4 during July and August was made up almost entirely of a dark green *Limnochironomus*. *T.* sp.—Three unidentified specimens of *Ten-*

dipes having one pair of gills on the eleventh abdominal segment were collected at station 6. *Chironomus* (*Endochironomus*) spp.—Two specimens of the subgenus *Endochironimus*, as defined by Johannsen (1937b), were collected at station 6 in July and August. *Polypedilum* (*Polypedilum*) *illinoense* (Malloch).—Rare in bottom samples. Three specimens collected from deep water stations and four specimens from sand and clay bottom at station 5. *P.* sp.—Several specimens of an undetermined *Polypedilum* were collected at stations 5 and 6. *Glyptotendipes* (*Glyptotendipes*) *senilis* (Johannsen).—Rare in bottom samples. Four specimens collected on sand and gravel bottom at station 4 in July. *Cryptochironemus digitatus* (Malloch).—Most abundant and widespread tendipedid collected in the bottom samples at Lizard Lake. Only a few specimens were collected at station 6 but it was abundant at all other stations throughout the sampling period. *Tanytarsus* spp.—Although not abundant this genus was widespread and a few specimens were collected at each of the stations.

HYDRACARINA

Aquatic mites are very difficult to pick from preserved samples and most of them were undoubtedly missed. They occurred in samples from all types of habitat sampled.

QUANTITATIVE ANALYSIS OF THE BOTTOM FAUNA

Because of the large amount of variation between samples taken at the same station the data used in the following analysis probably only give a rough approximation of the true conditions existing in the lake during the sampling period.

DEEP WATER STATIONS

The Tendipedidae or midges, comprising 93.43 percent of the dry weight and 78.57 percent of the numbers were by far the dominant group in the deeper water (table 3). The scud, *Hyalella knickerbockeri*, comprised 13.57 percent of the total number of organisms but contributed only 1.47 percent to the dry weight because of its small size. The other organisms found in the deeper water contributed very little to the total quantity.

Although conditions at stations 2 and 3 appeared to be very similar in regard to bottom soils and vegetation there was a wide difference in the aver-

TABLE 3.—Average dry weight and numbers of organisms per square meter for the deep water stations

	Weight (mg)	Percent	Number	Percent
Tendipedidae	1,280.00	93.44	1,210.00	78.57
Gastropoda	28.30	2.07	39.30	2.55
Oligochaeta	22.30	1.63	34.40	2.23
Hyalella	20.10	1.47	209.00	13.57
Heleidae	6.71	0.50	20.80	1.35
Zygoptera	5.67	0.41	10.90	0.70
Trichoptera	3.64	0.27	7.52	0.49
All others	2.87	0.21	8.35	0.54
Total	1,370		1,540	

age dry weight of organisms at these two stations (table 4). Station 2 supported a greater dry weight of bottom fauna although there was little difference in the average number of organisms at the two stations.

Station 2 and 3 were compared by the method of analysis of variance on the basis of total dry weight for each month in which samples were taken. The results (table 5) indicate that there was a significant difference between the stations in July and August and that the populations were very similar in September and October. The difference in dry weight of organisms at these stations during July and August was caused by the large bloodworm, *Tendipes* (= *Chironomus*) *tentans*, which is the largest tendipedid found in the lake. This species was very abundant at station 2 during July but few were taken in the dredge samples at station 3. In the latter part of July and in early August this species emerged and very few were taken in the dredge samples during September and October at either station.

The maximum numbers and dry weight of bottom fauna per square meter at the deeper water stations were found during the month of July with the minimum during September (fig. 2). The October dredgings showed a large increase in numbers but a very small increase in dry weight. Since the fauna of the deep water stations is composed largely of the larvae of Tendipedidae the variation in total fauna follows the variation in this group. The steep fluctuations in the quantity of bottom fauna from month to month can be

TABLE 4.—Average number and dry weight of bottom fauna per square meter at stations 2 and 3 during July, August, September and October, 1951

Station	Number	Weight (mg)
2	1,575	1,873
3	1,517	870

TABLE 5.—Analysis of variance for stations 2 and 3 on the basis of milligrams dry weight per square meter

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Ignoring months			
Between stations	1	32,075,992	32,075,992*
Within stations	57	86,268,534	1,513,483
July			
Between stations	1	17,532,160	17,532,160*
Within stations	11	8,053,684	732,153
August			
Between stations	1	2,545,465	2,545,465*
Within stations	15	7,872,820	524,855
September			
Between stations	1	20,085	20,085
Within stations	18	752,413	41,801
October			
Between stations	1	14,553	14,553
Within stations	7	910,714	130,102

* Significant at 5 percent level.

explained by the annual life cycle of tendipedid egg, larvae, pupae and emergence.

The minimum at the deep water stations in Lizard Lake was reached in September after the emergence of *Tendipes tentans*. Other species grew into the fauna during October causing a slight increase. That these specimens were small early instar larvae is indicated by the very slight increase in weight as compared with the increase in numbers (fig. 2). Although it cannot be definitely established with the present data it appears that the October increase is due to the growth into the fauna of early spring and early summer emerging species. The maxima in both numbers and weight would probably be reached in early spring before the emergence of these species and after the growth of *Tendipes tentans* back into the fauna.

SHALLOW WATER STATIONS

The shore area of Lizard Lake is a region of extreme variation in habitat and as a result almost all of the major groups of aquatic organisms normally found in a lake are represented (table 7). No single group completely dominated this region as was found to be true in the deeper water. The first four groups, Tendipedidae, Gastropoda, Oligochaeta and *Hyalella* are the same but there is a great deal of difference in their relative proportions as compared with the deep water stations. The Gastropoda are the dominant group contrib-

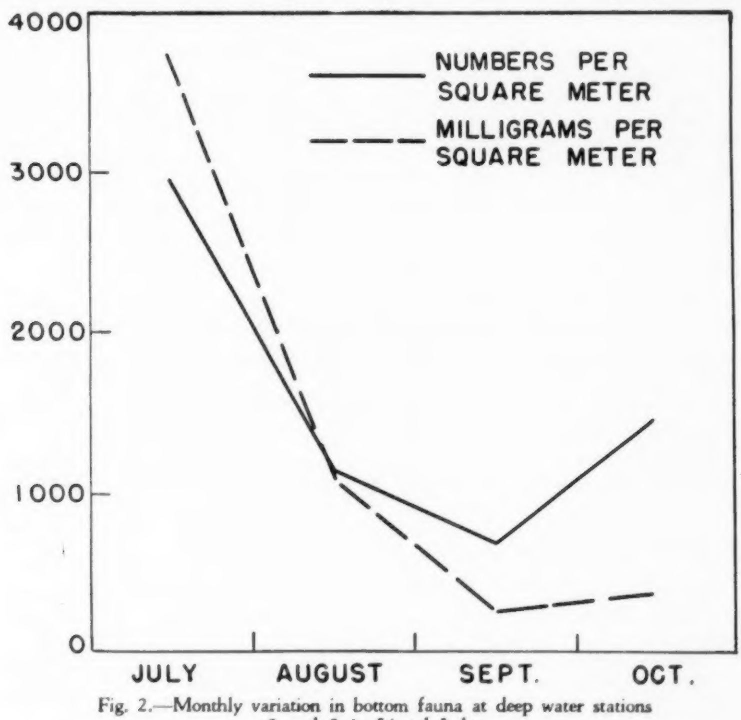

Fig. 2.—Monthly variation in bottom fauna at deep water stations 2 and 3 in Lizard Lake.

uting 36.23 percent to the total dry weight. The Tendipedidae are very numerous but are represented by small species. The "Other Diptera" listed in Table 6 are unidentified puparia which were abundant at some of the stations but were not present in deep water

Comparison of the stations.—The three shore stations, selected for study as represented of the major types of habitat in Lizard, were compared by the method of analysis of variance on the basis of dry weight in milligrams per square meter. (table 7). The calculated F values are significant at the 5 percent level for each month in which samples were taken. This means that we can reject a hypothesis that the populations at all three stations are the same, with the probability that less than 5 percent of the time we would be wrong in rejecting such a hypothesis. As was true for the deep water stations the differences between stations were due mainly to the size of the organisms rather than any great differences in numbers (table 8).

The uneven gravel bottom at station 4 yielded the largest number of organ-

TABLE 6.—Average dry weight and numbers of organisms per square meter for the Stations 4, 5, and 6.

	Weight (mg)	Percent	Number	Percent
Gastropoda	255	36.23	391	10.24
Tendipedidae	483	19.12	1,160	30.41
Oligochaeta	235	17.62	436	11.44
Hyalella	131	9.82	1,400	36.69
Anisoptera	63.2	4.74	8.73	0.23
Other Diptera	47.1	3.53	49.5	1.30
Baetidae	39.6	2.97	191	5.00
Corixidae	34.6	2.59	87.6	2.29
Zygoptera	15.7	1.18	21.1	0.55
Trichoptera	9.78	0.73	17.9	0.47
Notonectidae	8.11	0.61	3.52	0.09
Coleoptera	4.93	0.37	5.47	0.14
Heleidae	4.31	0.32	37.2	0.97
Nematoda	2.32	0.17	6.81	0.18
Total	1,334		3,819	

TABLE 7.—Analysis of variance for stations 4, 5 and 6 on the basis of milligrams dry weight per square meter.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Ignoring Months			
Between stations	2	23,128,647	11,564,324*
Within stations	82	149,228,876	1,819,864
July			
Between stations	2	27,434,132	13,717,066*
Within stations	12	23,862,861	1,988,572
August			
Between stations	2	8,720,005	4,360,002*
Within stations	22	12,110,808	550,491
September			
Between stations	2	22,068,439	11,034,219*
Within stations	42	57,133,480	1,360,321

* Significant at the 5 percent level.

isms and all the major groups found in the lake were represented at this station. Rawson (1930) found that in Lake Simcoe the highest populations of bottom organisms were in the protected stony bays. In Lizard Lake this type of habitat is most closely approximated by conditions at station 4 where the gravel bottom provides a large surface area of habitat for the bottom organisms. Small larvae of Tendipedidae, Oligochaeta and the naiads of the mayfly family Baetidae were the dominant organisms at station 4.

The quantity of bottom fauna from the heavily vegetated peat bottom at station 6 was much higher on a basis of total dry weight because of the large bloodworm, *Tendipes tentans*, which was very abundant on this type of bottom. Another factor contributing to the high average weight were the Odonata which were most abundant at station 6 and contributed disproportionately to the total weight in relation to their numbers.

The sand and clay bottom at station 5 was the poorest producer of bottom fauna on the basis of dry weight. The abundance of *Hyalella* sp. and Corixidae on the filamentous algae at this station resulted in the high numerical count (3,856 per square meter).

After the maximum in July there were no major fluctuations in the weight of the shallow water fauna (fig. 3), due to the small size of the majority of the species represented and to the overlapping in the periods of abundance of many different species. The high value in July was mainly a result of the very marked abundance of Tendipedidae (7,350 per square meter) at station 4.

There were sharp fluctuations in numbers of organisms from month to month in the shallow water zone with a maximum in July and a minimum value during October (fig. 3). The sharp increase in September was caused by several factors. Mayflies were very abundant at station 4 during September and most of them had emerged before samples were taken in October. Large mats of filamentous algae had settled to the bottom at station 5 in September and this algae was swarming with the small crustacean, *Hyalella knickerbockeri*. The bottom samples taken at this station in September gave an estimate of 5,410 *Hyalella* per square meter.

SUMMARY

Bottom samples were collected during the period from July 9 to October 6, 1951, at two deep water stations and three shallow water stations which are believed to be representative of the major types of habitat in Lizard Lake.

The magnitude of variation between samples was so great that any quantitative generalizations may be subject to a great deal of error.

A statistical comparison of the Petersen, Dendy and stovepipe methods of sampling indicated that there was no appreciable difference in the quantity of bottom fauna as estimated by these three samplers on a sand and gravel bottom.

The number of samples required to keep the standard error within 10 per-

TABLE 8.—Average number and dry weight of bottom fauna per square meter at Stations 4, 5 and 6 during July, August, September and October, 1951

Station	Number	Weight (mg)
4	4,108	1,297
5	3,856	671
6	3,497	1,846

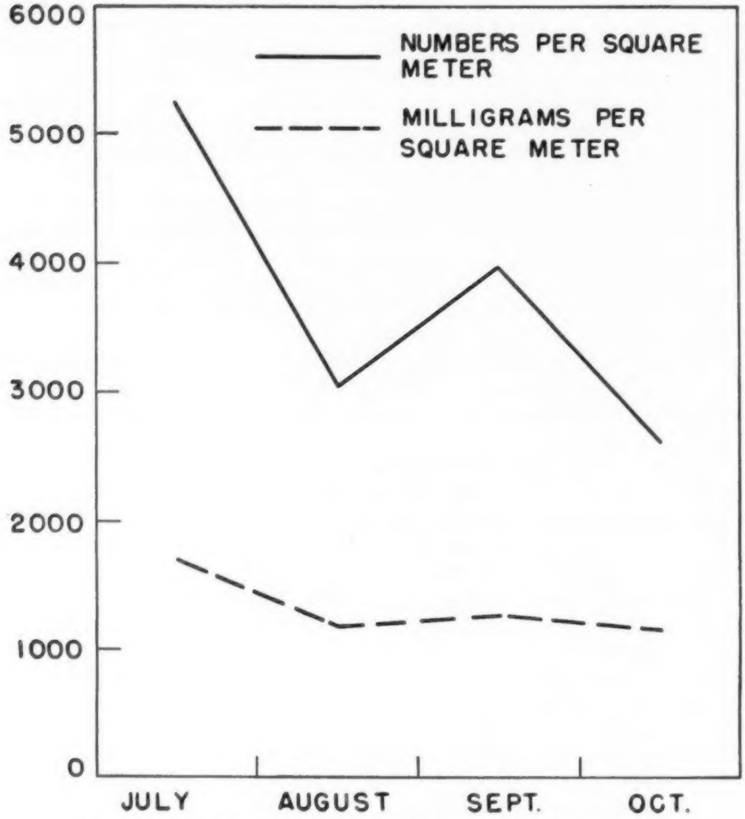

Fig. 3.—Monthly variation in bottom fauna at shallow water stations 4, 5 and 6, Lizard Lake.

cent of the mean was found to be 1,658 for the Dendy, 486 for the Ekman, 54 for the stovepipe and 19 for the Petersen.

On the basis of average dry weight of organisms the greatest quantities of bottom fauna were produced on the pulpy peat bottom in the deeper part of the lake (1,873 mg per square meter) and on the fibrous peat bottom in a heavily vegetated bay (1,846 mg per square meter).

A bottom composed of sand and clay produced the lowest average quantity of bottom fauna (671 mg per square meter).

A sand and gravel bottom in shallow water produced the largest numbers (4,108 per square meter) and kinds of organisms but was intermediate on the basis of average dry weight (1,297 mg per square meter), because of the small average size of the organisms represented.

The peak of abundance occurred in July with the minima in September or October.

The Tendipedidae were the most abundant group of aquatic invertebrates

and comprised 93.44 percent of the total dry weight at the deep water stations.

Gastropoda (36.23 percent), Tendipedidae (19.12 percent) and Oligochaeta (17.62 percent) were the most important components of the bottom fauna at the shallow water stations.

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Populations of the Genus Drosophila in the Great Smoky Mountains, Tennessee

John M. Carpenter* and Joseph F. Giordano
The University of Tennessee, Knoxville

The last decade has revealed a mounting interest in the collection and study of natural populations of various Drosophila species. However, few studies of the numerous species of the genus in the Great Smoky Mountains area have been published. It is, consequently, the purpose of this paper to report a study of such populations in this very important ecological area with the idea of pointing out the differences in population fluctuation associated with season of collection and altitude.

Patterson (1943) investigated the monthly fluctuations of various Drosophila populations at Aldrich Farm Plot, near Austin, Texas. He concluded that there were significant changes in population size of nine species and three complexes resulting from environmental factors. The environmental factors considered were chiefly climatic in nature. It was also demonstrated that these factors were different for different species.

Dobzhansky and Epling (1944) investigated the population fluctuations of *D. pseudoobscura* at four localities on Mount Jacinto, California, forming a climatic gradient up the mountain. The fluctuations observed were attributed to climatic factors. It was concluded that the relative increase or decrease of a population is a function of temperature and to a limited extent a function of rainfall. The existence of genetically different ecological types within the altitudinal gradient was demonstrated.

With the establishment in the literature of such a definite correlation between genetically different ecological types and altitude, Stalker and Carson (1948) undertook a study of the chromosome inversion frequencies in *D. robusta* collected from an altitudinal transect in the Great Smoky Mountain National Park, Tennessee. They set out a series of eight collecting stations between 1200 and 6300 feet. It was found that those stations located at an altitude of 6000 and 5000 feet did not yield *D. robusta* specimens and that specimens were uncommon at the 4000 foot level.

Speiss (1949) studied the monthly population fluctuations of various Drosophila species in the New England States. It was found that fluctuations resulting from seasonal changes involved variation in temperature and rainfall. His report states that, "temperature is apparently one of the most effective ecological factors in the distribution of these populations." However, contrary to Patterson's report his data supports the view that there is a negative correlation between humidity and the number of individuals in a population.

Spencer (1950), collecting at Jackson Hole, Wyoming at elevations between 6700 and 9675 feet, found fewer flies at the higher elevations. He collected a total of only five native species. This small number Spencer

* Present address: Department of Zoology, University of Kentucky, Lexington.

believes to be correlated with high altitude and northern latitude. Different species predominated in the several different ecological habitats sampled.

Stevenson (1952), studying species of Drosophila on Unaka Mountain in eastern Tennessee, found marked fluctuations in numbers from month to month. The significance of altitude is not made clear from his preliminary study, but, in general, he collected fewer species at higher altitudes.

Williams and Miller (1952), collecting in Nebraska, confirm the reports of other workers in observing seasonal variation in the frequencies of some of the species collected.

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METHODS OF COLLECTING

The collections on which the present study are based were made from July 1 to October 26, 1950 in the Great Smoky Mountains, Tennessee. A total of ten trapping sites were selected. Five of these were located between Rich Mountain (near Townsend, Tennessee) and Abrams Creek on the western edge of Cades Cove. Approximately 26 miles east of Cades Cove five other trapping sites were selected between the 2000 foot roadside marker above Park Headquarters, 2 miles south of Gatlinburg, and Clingmans Dome (elevation 6642 feet). For the sake of convenience the region of the first five traps is referred to as Cades Cove and that of the second five traps as the Smokies. Cades Cove is a relatively isolated area which is almost inaccessible by automobile during some months of the year while the Smokies are visited by more than 2 million persons annually via its well paved roads.

CADES COVE COLLECTION

On June 24, 1950 a reconnaissance of the area was undertaken as to the possibilities of collecting Drosophila in the region. Suitable collecting sites were selected within walking distance of the road and were assigned station numbers corresponding to their roadside position leading towards the cove. Whenever possible all traps were placed in cool, moist, dense woods which would afford them continuous shade. Several readings were made from an altimeter throughout the collecting period, and an average of the readings was used as the standard elevation for the various stations.

Collections were begun on July 1. The method, similiar to Patterson, (1943), was as follows: Fifty pound lard cans were obtained, painted forest green and used as traps. Each of the five traps was then baited with over-ripe bananas which were placed in the bottom of the cans. Two thick sticks were then placed across the mouth of each can and a lid was placed on them which permitted the flies to enter through the opening around the rim of the can. It was found that this arrangement protected the traps from rain, and shaded the interior of the cans. During the initial collecting period the traps were visited twice a week but toward the end of August transportation difficulties arose and the remainder of the collections were made once a week. The traps were always visited in the

morning or early evening when temperatures are at a minimum. In order to remove the flies from the traps a nylon collecting net was used, the open end of which would fit tightly over the mouth of the baited traps. The lower end of the net was reduced to form a tube approximately one inch in diameter, and stiffened with a solution of celloidin.

The actual method by which the flies were collected is as follows: As the traps were approached, the net was inverted and held by the tube in the left hand while the other hand held the net handle. Care was taken not to make any noise lest the flies be disturbed and fly out of the traps. When the net was directly over the trap the lid and supporting sticks were quickly kicked off with the right foot and the open end of the net placed over the mouth of the trap. The can was then kicked gently with the foot several times causing most of the flies to rise into the net. The net was then removed and swung back and forth above the can several times thereby capturing the remaining flies while forcing them down into the tubular end. Flies were then transferred to one-half pint milk bottles and stoppered with cotton plugs. Bottles were placed in an auto ice box and taken back to the laboratory where they were transferred to bottles containing fresh food medium as reported by Carpenter (1950). On the same day and the following day (depending upon the number of specimens obtained) the flies were classified as to species and numbers with the aid of a binocular microscope, and a permanent record made including the collection date, station number, and number of individuals of each species.

The following description based on standard $\frac{1}{4}$ acre plots (centering at each trap) characterize some of the vegetational and topographic features of the collecting sites in Cades Cove.

Station C.C. 1 (*elevation*: 1150 *feet*).—A cut-over tract of land characterized by a steep northeast slope with very thin soil situated on the edge of an old field. The canopy was about 30 feet tall with the dominant tree species being black oak, and white pine. The principal undergrowth consisted of mountain laurel, and strawberry bush.

Station C.C. 2 (*elevation*: 2000 *feet*).—A cut-over stand situated in a ravine, principally in white pine, hemlock, and red maple reproduction. The broken canopy consisted of scarlet oak, black oak, and white oak remnants of the original forest, about 40 feet tall, with a heavy undergrowth of *Rhododendron maximum*, mountain laurel, and strawberry bush. (Distance from Station 1: 3.5 miles).

Station C.C. 3 (*elevation*: 2500 *feet*).—A stream bank in a ravine bottom. The broken canopy consisted of hemlock, chestnut, scarlet oak, and white oak remnants of the original forest about 40 feet tall. Principal undergrowth consisted of *Rhododendron maximum* and mountain laurel. (Distance from Station 2: 3.5 miles).

Station C.C. 4 (*elevation*: 1800 *feet*).—A successional stand with a sharp slope facing southeast and consisting mostly of white pine. Many decaying chestnut stumps lead to the conclusion that oak-chestnut was probably dominant at one time. The broken canopy was about 35 feet tall and consisted of black oak, northern red oak, chestnut oak, and southern

red oak which are remnants of the original forest stand. The undergrowth consisted mostly of American holly, spotted wintergreen, and trailing arbutus. (Distance from Station 3: 3.5 miles).

Station C.C. 5 (*elevation*: 2000 *feet*).—Near Abrams Creek on relatively flat land. The tract was in early stages of secondary succession, the principal reproduction consisting of pitch pine, white pine, and short-leaf pine with some yellow birch coming in. Principal undergrowth consisted of smooth sumac, *Rhododendron maximum*, and mountain laurel. (Distance from Station 4: 4.5 miles).

The entire transect extended over approximately 15 miles.

SMOKIES COLLECTION

The method of collecting employed in the Smokies area was essentially the same as that in Cades Cove. However, several differences in procedure should be noted: 1) collecting was begun on September 6, 1950; 2) only weekly visits to the traps were made throughout the entire collecting period; 3) roadside altitudinal markers were used for the establishment of collecting sites; 4) the early stages of collecting found tourists and bears occasionally upsetting the traps. However, this was remedied by heavily weighing down the lids and camouflaging the traps with small branches and leaves.

The following descriptions characterize some of the vegetational and topographic features of the collecting sites in the Smokies.

Station S2 (*elevation*: 2000 *feet*).—A steep well drained ravine that had been cut over for a long time. The canopy was approximately 25 feet tall with the dominant tree species being tulip poplar, yellow birch, red maple, and hemlock. The principal undergrowth consisted of *Rhododendron maximum* and elderberry.

Station S3 (*elevation*: 3000 *feet*).—A second growth stand with steep topography whose canopy was approximately 40 feet tall; the principal tree species being tulip poplar, silver bell, northern red oak, black locust, and sugar maple. A very dense layer of catbrier constituted the important ground cover layer. (Distance from Station S2: 3.5 miles).

Station S4 (*elevation*: 4000 *feet*).—A flat between two ravines. The 65 foot tall canopy consisted of yellow birch, buckeye, and some spruce and hemlock which was at one time part of the original canopy. The twenty foot layer consisted mainly of yellow birch with some red maple and black birch. The principal undergrowth was *Rhododendron maximum* and service berry. (Distance from Station S3. 3.5 miles).

Station S5 (*elevation*: 5000 *feet*).—A virgin stand situated on a very steep slope, the canopy consisting of spruce approximately 80 feet tall. The second layer (approximately 35 feet tall) consisted principally of black birch and beech. The important shrub species found were *Rhododendron maximum*, witch hobble, and mountain cranberry. (Distance from Station S4: 4 miles).

Station S6 (*elevation*: 6000 *feet*).—A steep slope in a typical virgin spruce-fir forest with many decaying trees and tree stumps. The principal

undergrowth consisted of scattered patches of mountain cranberry. (Distance from Station S5: 6.3 miles).

The entire transect extended over approximately 17.3 miles.

RESULTS

Seasonal Fluctuations, Cades Cove.—The population sample in Cades Cove consisted of 20,768 flies representing sixteen Drosophila species from twenty-two collections. The minimum number of flies was obtained during July and the maximum in September, although seven collections were made in July and only four in September. These data are shown in table 1.

TABLE 1.—Collection record: Cades Cove—Numbers and percentages of 16 species of Drosophila

Species	July No. %	August No. %	September No. %	October No. %	Total No. %
D. immigrans	221(12.0)	2511(51.8)	2902(40.8)	2638(37.8)	8272(39.8)
D. melanogaster	7(0.4)	31(0.6)	1892(26.6)	2717(39.0)	4647(22.4)
D. affinis subgroup	1400(75.9)	1018(21.0)	264(3.7)	110(1.6)	2792(13.4)
D. robusta	106(5.7)	652(13.5)	737(10.4)	641(9.2)	2136(10.3)
D. nigromelanica	62(3.4)	339(7.0)	753(10.6)	112(1.6)	1268(6.1)
D. hydei	4(0.0)	3(0.0)	277(3.9)	356(5.1)	639(3.1)
D. putrida	26(1.4)	50(1.0)	144(2.0)	168(2.4)	388(1.9)
D. melanica	9(0.0)	198(4.1)	9(0.0)	9(0.0)	225(1.1)
D. busckii		20(0.4)	102(1.4)	94(1.3)	216(1.0)
D. transversa	1(0.0)	7(0.0)	14(0.0)	83(1.2)	105(0.5)
D. tripunctata	8(0.0)	17(0.0)	7(0.0)	38(0.0)	70(0.3)
D. testacca				4(0.0)	4(0.0)
D. micromelanica	1(0.0)	1(0.0)	2(0.0)		4(0.0)
D. macrospina				2(0.0)	2(0.0)
D. sigmoides				1(0.0)	1(0.0)
D. guttifera				1(0.0)	1(0.0)
Totals	1845(8.8)	4847(23.3)	7103(34.2)	6973(33.5)	20,768
No. of Collections	7	7	4	4	22

Figures 1 and 2 show, by the use of histograms, monthly percentages of the common and rare species. A common species was considered to be one that appeared in the total collection at a figure of five percent or greater. A rare species was considered to be one that appeared at a figure smaller than five percent.

D. immigrans, a well known introduced species, was the most common and successful species during the months in which the collections were taken. It reached a population peak in August at which time 2511 flies, amounting to 51.8 percent of the entire monthly collection, were taken. A high population level was maintained throughout September and October.

D. melanogaster was found to be discontinuous and rare in occurrence during July and August; however, in September it appeared in considerable numbers, and reached a population peak in October. In point of number and percent, *D. melanogaster* is second in the list of species for the entire collection.

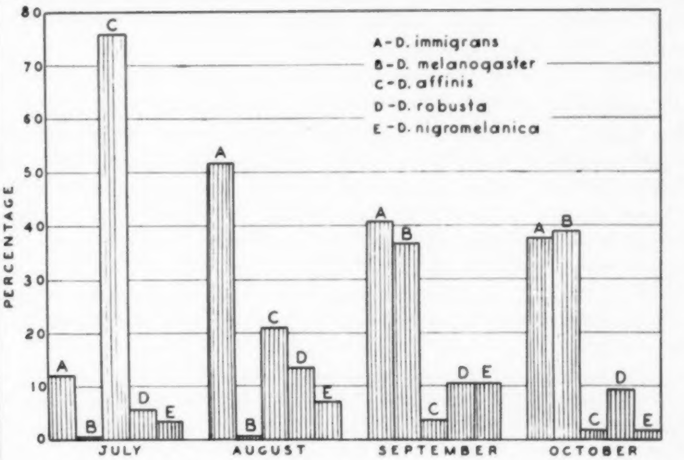

FIG. 1. TOTAL MONTHLY PERCENTAGE OF THE COMMONER SPECIES OF DROSOPHILA FOUND IN CADES COVE.

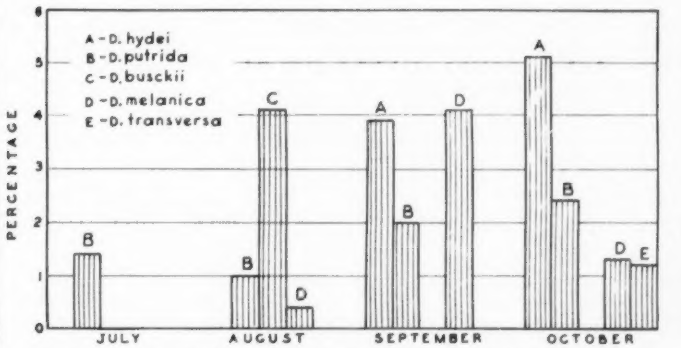

FIG. 2. TOTAL MONTHLY PERCENTAGE OF THE RARER SPECIES OF DROSOPHILA FOUND IN CADES COVE.

The *D. affinis* subgroup appears to have been at its population peak (75.9%) in July and then progressively decreased in numbers and percentage during the following three months to a population low of 1.6 percent in October. Members of this subgroup were found to be the most abundant wild species, although third in rank for the entire collection.

D. robusta, which was found to be sporadic in occurrence during July, suddenly reached a population peak in August, then slowly decreased in

percentage during September and October. In contrast, the *D. nigromelanica* population slowly increased during July and August, reached its peak in September, then dropped suddenly in October.

D. hydei was discontinuous and rare during July and August. In September the population suddenly increased and reached its peak in October.

D. putrida, one of the rarer species, appeared to be on its ascendency when the collections were begun in July. The population contracted slightly in August, then gradually expanded and reached a second peak in October.

D. melanica was found only sporadically during July, then suddenly reached a population peak in August and decreased to a percentage below one-tenth during September and October.

D. busckii was not collected during July. However, in August twenty individuals were obtained and a population peak of 1.5 percent was reached in September.

D. transversa and *D. tripunctata* were obtained throughout the four month collecting period, but were very sporadic and rare in occurrence. They were not found in sufficiently large enough numbers to determine population peaks.

TABLE 2.—Collection record: Cades Cove—Number of flies collected at five different stations

	Station Number and Elevation (ft.)					
Date	1 1150	2 2000	3 2500	4 1800	5 2000	Total
July 1	46	36	24	27	....	133
July 8	....	6	23	20	1	50
July 15	79	18	10	167	51	325
July 20	3	23	26	16	21	89
July 22	72	87	157	130	82	528
July 26	25	93	16	85	192	411
July 28	38	50	27	47	147	309
Total	263	313	283	492	494	1845
August 2	80	335	221	136	271	1043
August 5	20	206	296	202	105	829
August 9	81	337	180	28	238	864
August 11	44	167	90	50	198	549
August 16	71	199	69	77	145	561
August 25	69	75	70	104	103	421
August 30	49	222	101	63	145	580
Total	414	1541	1027	660	1205	4847
September 6	189	165	54	22	91	521
September 13	341	285	71	240	251	1188
September 20	629	381	184	260	1421	2875
September 26	453	708	310	544	504	2519
Total	1612	1539	619	1066	2267	7103
October 5	196	98	60	77	232	663
October 12	720	501	526	540	403	2690
October 19	485	439	407	421	489	2241
October 26	40	323	81	99	836	1379
Total	1441	1361	1074	1137	1960	6973
Grand Total	3730	4554	3003	3355	5926	20,768

D. micromelanica, D. macrospina, D. sigmoides, and *D. guttifera* are considered as very rare species. Only eight specimens representing these four species were obtained in the entire collection of 20,768 flies. *Macrospina, sigmoides, and guttifera* appeared in October, as the weather became cooler.

There appeared little difference in the numbers collected at the several altitudes (table 2). At the lowest altitude (1150 feet) a total of 3730 flies were collected while at the highest (2500 feet) a total of 3003 were collected. It is probable that climatic factors varied little throughout this small altitudinal range.

Seasonal Fluctuations, Smokies.—The population sample in the Smokies consisted of 5973 flies representing 15 Drosophila species from eight collections. The data in table 3 shows the species collected and their numbers on a monthly basis.

The largest number of flies was obtained during the month of October as compared to September for Cades Cove (table 3). *D. immigrans* was the most common species collected, followed by *melanogaster, busckii,* and *hydei* in that order. The *affinis* subgroup, *putrida,* and *robusta* were considered rare. The remaining eight species were found in such small numbers in the entire collection as to be considered very rare.

Applying the previously established figure for commonness and rareness

TABLE 3.—Collection record: Smokies—Numbers and percentages of 15 species of Drosophila

Species	September No. %	October No. %	Total No. %
D. immigrans	1435(50.6)	1561(49.7)	2996(50.2)
D. melanogaster	650(22.9)	980(31.2)	1630(27.3)
D. busckii	122(4.3)	230(7.3)	352(5.9)
D. hydei	199(7.0)	152(4.8)	351(5.9)
D. affinis subgroup	227(8.0)	24(0.8)	251(4.2)
D. putrida	134(4.7)	40(1.3)	174(2.9)
D. robusta	28(1.0)	116(3.7)	144(2.4)
D. nigromelanica	27(1.0)	11(0.4)	38(0.6)
D. sigmoides		14(0.4)	14(0.2)
D. transversa	4(0.1)	4(0.1)	8(0.1)
D. tripunctata		6(0.2)	6(0.1)
D. micromelanica	2(0.0)	1(0.0)	3(0.0)
M. melanica	1(0.0)	1(0.0)	2(0.0)
D. macrospina	2(0.0)		2(0.0)
D. magnafumosa	2(0.0)		2(0.0)
Total	2833(49.1)	3140(50.8)	5975
No. of Collections	4	4	8

on a monthly basis some interesting comparisons of certain species may be made with the Cades Cove collection (table 4). *D. robusta* and *nigromelanica,* both common species in Cades Cove in September were found rarely in the Smokies, whereas *hydei* and the *affinis* subgroup, found rarely during the same month in Cades Cove, were common in the Smokies. Other species were rare in both areas during September. *D. robusta* continued common in Cades Cove in October, but *nigromelanica* became rare; the *affinis* subgroup continued rare. *D. hydei* shifted from a rare to a common species.

In the Smokies, the *affinis* subgroup became rare in October. *D. hydei* became a borderline case. *D. robusta* continued rare but *busckii* rose to the status of a common species.

TABLE 4.—Comparison of September and October collections in Cades Cove and Smokies

Cades Cove	%	Smokies	%
	September		
D. nigromelanica	10.6	D. affinis subgroup	8.0
D. robusta	10.4	D. hydei	7.0
D. hydei	3.9	D. putrida	4.7
D. affinis subgroup	3.7	D. busckii	4.3
D. putrida	2.0	D. robusta	1.0
D. busckii	1.4	D. nigromelanica	1.0
	October		
D. robusta	9.2	D. busckii	7.3
D. hydei	5.1	D. hydei	4.8
D. putrida	2.4	D. robusta	3.7
D. affinis subgroup	1.6	D. putrida	1.3
D. nigromelanica	1.6	D. affinis subgroup	0.8
D. busckii	1.5	D. nigromelanica	0.4

It was found that the number of flies collected varied inversely with altitude. Of the total of 5973 flies collected, 2436 were collected at 2000 feet, 2022 at 3000 feet, 892 at 4000 feet, 372 at 5000 feet and 251 at 6000 feet (table 5). This trend was not seen at Cades Cove. This appears to be because all altitudes were below 3000 feet in Cades Cove and a decrease in numbers was shown beginning only at 4000 feet (in the Smokies).

Altitudinal Fluctuations.—Since the Smokies represented the only area in which a wide altitudinal range was found it was decided that figures from this area would be of most significance in a study of altitudinal fluctuations.

TABLE 5.—Collection record: Smokies—Number of flies collected at five different stations

Date	Station Number and Elevation (ft.) S2 2000	S3 3000	S4 4000	S5 5000	S6 6000	Total
September 6	14	63	0	0	9	86
September 13	307	306	53	0	62	728
September 20	228	371	145	20	137	901
September 26	160	571	169	185	33	1118
Total	709	1311	367	205	241	2833
October 5	66	110	156	13	0	345
October 12	513	389	61	21	7	991
October 19	524	165	308	15	1	1013
October 26	624	47	0	118	2	791
Total	1727	711	525	167	10	3140
Grand Total	2436	2022	892	372	251	5973

The percentages of the commoner species of Drosophila found in the Smokies were plotted against the September and October collection dates at five station altitudes. The results are presented in the form of five graphs in fig. 3. Accompanying each of the graphs is a series of histograms representing the total percentages of each species at the various altitudes.

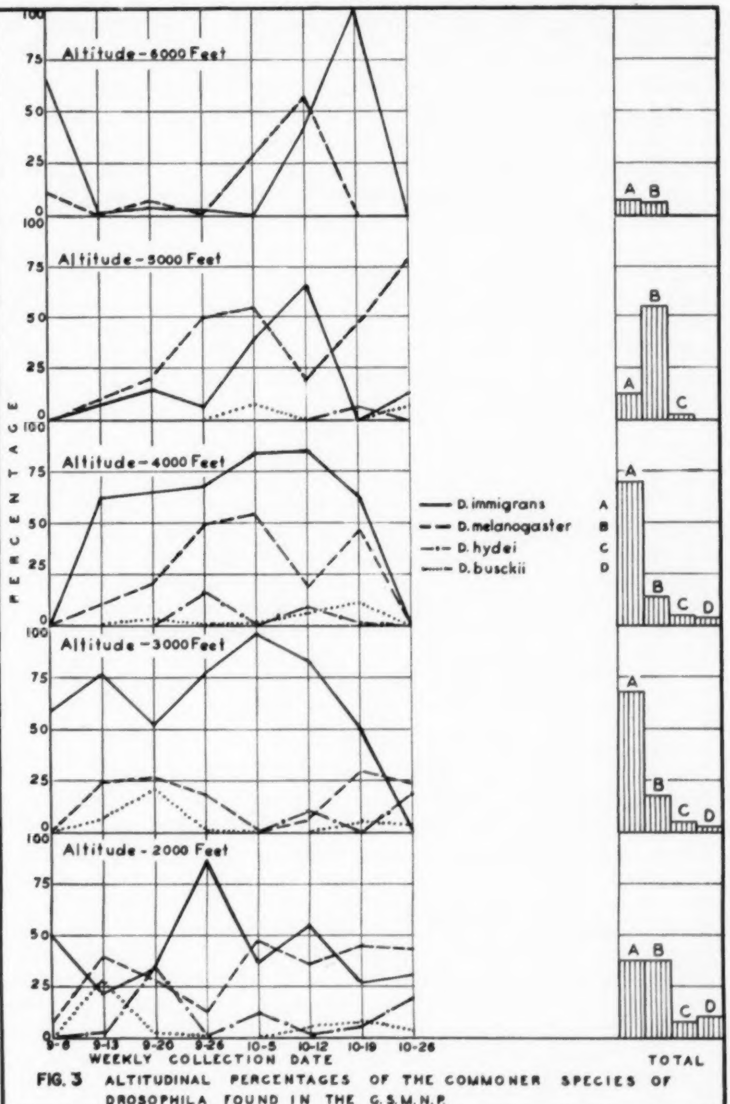

FIG. 3 ALTITUDINAL PERCENTAGES OF THE COMMONER SPECIES OF DROSOPHILA FOUND IN THE G.S.M.N.P.

D. immigrans was obtained in all collections at S2 and was obtained in the majority of the collections at the higher elevations. Several population peaks are demonstrable at all elevations (fig. 3). Although *D. immigrans* was the most common species found at most altitudes the histograms show that there is a decrease in population size at the higher elevations.

D. melanogaster presents several population peaks at station S2 which correspond to the *D. immigrans* population low points. Population peaks for *D. melanogaster* may be seen at all altitudes. However, beginning at

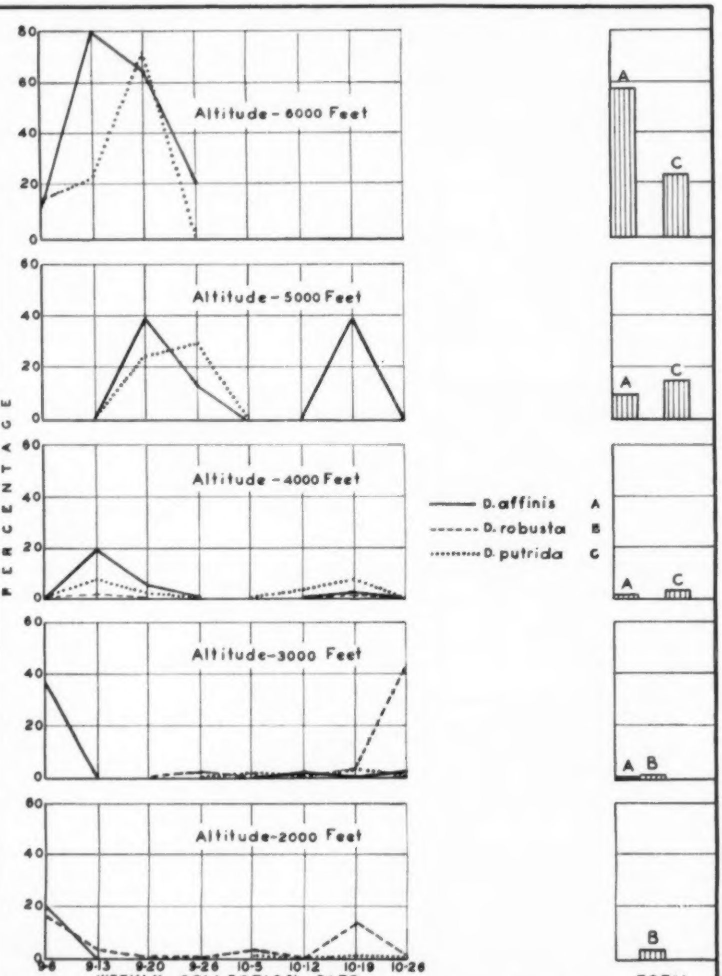

FIG. 4 ALTITUDINAL PERCENTAGES OF THE RARER SPECIES OF DROSOPHILA FOUND IN THE G.S.M.N.P.

2000 feet and extending to 4000 feet there was a continual decrease in the population sizes at those altitudes. At 5000 feet there was a sudden increase in population size and then a sharp decrease at 6000 feet

Due to the small numbers of *D. hydei* specimens collected, the population peaks for most elevations are not prominently displayed in fig. 3. However, the sudden contraction and expansion of this species at these elevations created sharp peaks which were not apparent in the other species population peaks. The percentage decrease of the *D. hydei* populations with increase in altitude appears to be very gradual and terminates in a zero population at 6000 feet.

Population peaks for *D. busckii* and *D. melanogaster* may be seen to occur on the same collection dates at all elevations except 6000 feet. *D. busckii* also exhibits a decrease in population size at the higher elevations. This species was not found at 6000 feet.

In fig. 4 the rarer species of Drosophila are presented graphically in the same manner as those in Figure 3.

The population size of the *affinis* subgroup at 2000 and 3000 feet was not significant enough to determine any population peaks. With an increase in altitude the numbers of specimens obtained increased, and at 6000 feet 59 percent of the total collection was occupied by this subgroup. Conversely the *D. robusta* population was zero at 6000 feet and only one specimen was collected at 5000 feet, although it was fairly abundant at the lower altitudes.

D. putrida shows the same altitudinal relationship as the *affinis* subgroup, with the maximum number of specimens obtained at 5000 and 6000 feet although none of the specimens were collected during October.

The following observations pertain to the very rare species of Drosophila collected in the Smokies: 1) during September *D. nigromelanica* was not collected at station S4, S5, and S6, and none were collected during October at Station S4; 2) fourteen specimens of *D. sigmoides* were collected during October at station S3 and S4; 3) *D. transversa* was found during September and October at station S2 and S3; 4) *D. micromelanica* and *D. magnafumosa* were collected only at station S6.

DISCUSSION

Shanks (1950) found that there occurred definite changes in temperature and precipitation throughout the transect on which the present study of the Smokies area is based. He has shown that there is a sharp decrease in temperature and increase in precipitation with an increase in elevation. The nature of the precipation and temperature is such that the former has increased by 50 percent by the time the spruce-fir zone is reached as compared to the base of the mountain, and the average rate of temperature decrease with altitude is 2.23°F per thousand feet. During the summer months the spruce-fir forest averages 10 to 15° cooler than Park Headquarters. There is also a sharp cooling between October and November which was responsible for the termination of collecting trips in the Smokies. From the results on which the present study is based it is, therefore, clear that the role of many different ecological factors and their consequent vegetational and topographical patterns which are distributed throughout this transect

are of considerable importance in determining the nature of species and their population sizes at the various elevations. Temperature and precipitation data were not available for Cades Cove; however, a comparison of the results obtained in Cades Cove with those in the Smokies shows some interesting parallels and differences.

Sixteen species of Drosophila were found in Cades Cove, of which two (*D. testacea* and *D. guttifera*) were not found in the Smokies. One of the species, *D. magnafumosa,* believed to be endemic at high altitudes in the Smokies, was collected only at station S6 (elevation: 6000 feet). This species has also been obtained by Spencer (personal communication), and only at an altitude of 6000 feet in the Smokies. However, *magnafumosa* has recently been taken at 3760 feet in July by Stevenson (1952) in the Unaka Mountains near Johnson City, Tennessee. Nothing is known of its food habits or breeding habits, and it has not been possible to rear it successfully in the laboratory. Furthermore, specimens of this species have never been collected in numbers large enough to warrant statistical treatment.

D. immigrans and *D. melanogaster* are the most common species in both Cades Cove and the Smokies. On the other hand, *busckii* and *hydei* ranked third and fourth in importance in the Smokies while these same species were replaced by the *affinis* subgroup and *D. robusta* in importance at Cades Cove. A possible explanation may be the relative isolation of Cades Cove as compared to the close association of the domestic species *D. busckii* and *D. hydei* in the Smokies with human agencies.

The *D. affinis* subgroup also appears to be more successful during the cooler months and at the higher altitudes in the Smokies. The competition for food and space which is lacking at an elevation of 6000 feet because of the absence of other more aggressive species may be the reason for its successfulness at this elevation.

The seasonal fluctuation of this subgroup as compared to the introduced species *immigrans* and *melanogaster* is an interesting case. This subgroup comprised almost 76 percent of the population at Cades Cove during July (table 1) after which it became progressively less common during the remainder of the season until it comprised only 1.6 percent of the population in October. On the other hand, *immigrans* and *melanogaster* comprised only 12 percent and 0.4 percent, respectively, of the population in July, but increased rapidly in percentage to a combined total of almost 77 percent of the entire population in October. That the *affinis* sub-group prefers cooler temperatures, whether due to seasonal or altitudinal causes, is shown by the fact that it was consistently taken in fairly large numbers at the higher elevations of the Smokies (fig. 6). This same seasonal fluctuation has been shown recently by Spiess (1949) for the New England states, Stevenson (1952) for the Unaka Mountains in Tennessee, and Williams and Miller (1952) for the state of Nebraska.

D. robusta was found to be at the higher altitudes in the Smokies. Stalker and Carson (1948) reported an absence of *D. robusta* specimens at 5000 and 6000 feet. This absence was attributed to the nature of the vegetation at these altitudes which is predominantly spruce-fir. Carson and Stalker (1951) concluded that the natural breeding sites of *D. robusta* are slime fluxes and exudations from injured hardwood trees.

D. putrida was obtained from collecting traps, and also bred from several species of fungi which were brought to the laboratory. The fungi were collected on several occasions throughout the transect at Cades Cove. It was found that *D. putrida* was not obtained as consistently as *D. transversa* and *D. tripunctata*. These findings are in agreement with those of Carson and Stalker (1951). Patterson (1943) states that *D. putrida* is a fungus feeder and has inferred that the population peaks of *D. putrida* in Texas coincide with increased rainfall which tends to increase fungus growth. The observations on which the present study are based indicate that the *D. putrida* population percent is greater at the higher altitudes in the Smokies. It is suggested that the nature of the vegetation, the low temperature, and the high precipitation (over 80 inches, annually) at the 5000 and 6000 feet stations in the Smokies supports comparatively little fungus growth. This is borne out by observations made by the writers. If *D. putrida* is primarily a fungus feeder, it seems odd that there was found such a large population percentage at these altitudes. The writers are of the opinion that some natural breeding substance other than fungi, the lack of other species competition, and a preference for cooler regions contributes to the success of *D. putrida* at the higher altitudes.

Those species which were represented by less than one percent in the total sample population in Cades Cove and the Smokies are considered as very rare species and were only locally important. However, it may be that these species were only mildly attracted to the traps or enter them only by chance. There is also a possibility that some species which would be attracted to the traps were not collected because their population level was so near zero that they did not enter the traps by chance.

The most productive collecting months were September and October. Two-thirds of the specimens (67.8%), representing 14,076 flies were taken in Cades Cove during these months from eight collections out of a total of twenty-two (table 1).

On the basis of altitude, stations at altitudes not exceeding 3000 feet were productive of larger populations. In the Smokies, during September and October, station 2 (elevation: 2000 feet) yielded 2432 flies and station 3 (elevation: 3000 feet) yielded 2022 for a combined total yield of 4458. The combined total yield during these months from stations at 4000, 5000, and 6000 feet was only 1515 flies.

That these figures are trustworthy is borne out by the Cades Cove data where at stations 1, 2, 3, 4, 5, representing elevations of 1150, 2000, 2500, 1800, and 2000 feet respectively, collections of 3053, 2900, 1693, 2203, and 4227, respectively, were taken during these two months. These are figures which approach those above for flies taken at comparable altitudes and by comparable collecting techniques in the Smokies.

SUMMARY

Drosophila population samples were collected during a period of four months at ten stations in the Great Smoky Mountains, Tennessee. Stations ranged in altitude from 1150 to 6000 feet and varied greatly in vegetation and other ecological factors concerned with their habitats. The greatest

number of specimens was taken during the months of September and October.

A total of seventeen species was found. One of these, (*D. magnafumosa*), was taken only at an elevation of 6000 feet. It was found that the total number of flies taken varied inversely with altitude.

Monthly population peaks were definitely demonstrable for certain species in the area of Cades Cove. Other species were not collected in sufficiently large enough numbers for their peaks to be statistically useful.

Altitudinal population fluctuations of the various species were observed. Of the species considered, only the *affinis* subgroup and *D. putrida* were found to increase in population percent with altitude.

It is suggested that the variability of the ecological factors may be responsible for the monthly population peaks and altitudinal fluctuations exhibited throughout the areas collected.

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The Ant Larvae of the Myrmicine Tribe Solenopsidini[1]

George C. Wheeler and Jeanette Wheeler
University of North Dakota, Grand Forks

We define this tribe to include the following 26 genera: *Vollenhovia, Gauromyrmex, Heteromyrmex, Huberia, Monomorium, Epixenus, Trichomyrmex, Hagioxenus, Wheeleriella, Phacota, Paraphacota, Xenomyrmex, Allomerus, Megalomyrmex, Liomyrmex, Epoecus, Anergates, Anergatides, Bruchomyrma, Tranopelta, Tranopeltoides, Carebarella, Carebarelloides, Diplomorium, Bondroitia, Solenopsis.* Only nine of these genera are represented in our collection, which includes a total of 21 species. References from the literature for three additional genera and eleven additional species make a total of 12 genera and 32 species treated in this article.

Included in the Solenopsidini are some very interesting ants. *Allomerus* nests in natural plant cavities in humid neotropical forests; the sexual larvae are markedly different from the worker larvae. Several genera are workerless social parasites: *Anergates, Anergatides, Bruchomyrma, Epixenus, Epoecus, Hagioxenus, Trichomyrmex* and *Wheeleriella.* The largest genus in the tribe is *Monomorium;* next is *Solenopsis.* These two genera have provided mankind with several of its annoying pests. Three are common household pests in the United States: *Monomorium minimum, M. pharaonis* and *Solenopsis molesta.* Concerning the polymorphic species, *Solenopsis geminata* and *S. saevissima,* Creighton[2] has written:

Fire ants of another species (*Solenopsis xyloni*) are similarly injurious and sometimes also become house pests. Several of the small monomorphic species of *Solenopsis* are known to be thief ants; they nest near the galleries of larger ants and steal the food and brood of the latter.

Wheeler[3] once wrote that the tribe Solenopsidini was "very unsatisfactorily defined." After studying the larvae, we heartily agree, for they are a very heterogeneous lot. To be sure, the larvae of *Monomorium s. str.* can scarcely be distinguished from those of *Solenopsis;* but aside from these two, we can detect no affinities. The nine genera studied might just as well be in eight different tribes. We have not been able to find any characters common to all the genera; hence we have not even attempted a characterization of the tribe.

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[1] The research on which this article is based was aided by a grant-in-aid from the Sigma Xi-Resa Research Fund.

[2] Bull. Mus. Comp. Zool. Harvard 104:227. 1950.

"The workers forage actively and are pugnacious in the extreme. They have a particularly painful sting which accounts for their popular name of 'fire ant.' Wherever they occur they are a dominant note in the environmental picture and they are among the few species of ants which can justifiably be regarded as serious pests. Because of their omnivorous habits they are always turning up in unexpected situations. They have been known to damage the buds and tender twigs of young fruit trees and kill quail which are too young to leave the nest. In certain areas they are a chronic nuisance because their unsightly nests disfigure lawns."

[3] Bull. Amer. Mus. Nat. Hist. 45:659. 1922.

VOLLENHOVIA Mayr

Comparatively slender; thorax stout and curved ventrally to about 90°; no neck; abdomen nearly straight. Body nearly naked; hairs exceedingly few; anchor-tipped hairs absent. Antennae small. Head hairs few; no hairs on clypeus. Labrum short and broad, slightly curved; posterior surface spinulose, the spinules minute and in short transverse rows. Mandibles rather long and slender; apex forming a rather long slender tooth which is slightly curved medially and posteriorly; medial teeth near the anterior surface, moderately large and curved posteriorly; posterior and medial surfaces with a few denticles. Maxillary palp a slightly raised disc; galea subcylindrical, with the end rounded. Labium broad and feebly trilobed; the anterior surface spinulose, the spinules minute and in short transverse rows. Dorsal portion of hypopharynx with sublongitudinal ridges; ventral portion spinulose, the spinules minute and in short transverse rows.

VOLLENHOVIA sp.

Pl. I, figs. 1-6

Comparatively slender; thorax stout and curved ventrally to about 90°; no neck; abdomen nearly straight. Dorsal profile curved, ventral nearly straight. Posterior end round. Anus ventral. Leg and wing vestiges present. Spiracles small, the first slightly larger. Segmentation distinct. The ventral surface of the thorax and first abdominal somite sparsely spinulose, the spinules minute and in short transverse rows. Body nearly naked; hairs exceedingly few. Of two types: 1) short (about 0.072 mm), with bifid tip, limited to the ventral surface of the prothorax (six hairs) and of the mesothorax (four hairs); 2) a very few widely scattered simple minute hairs, 0.001-0.009 mm long. Head subpyriform in anterior view; breadth of cranium equal to length. Antennae small, with three sensilla, each of which bears a spinule. Head hairs few, rather long (about 0.072 mm), with the tip bifid; however, as many as 3-4 long hairs may be replaced by minute simple hairs about 0.009 mm long; no hairs on the clypeus. Labrum short (breadth 3x length); length uniform; slightly curved; anterior surface with six minute sensilla; ventral border with two isolated sensilla and two clusters of three sensilla each; posterior surface of each half with three isolated sensilla and a cluster of three sensilla; posterior surface spinulose, the spinules minute and in short transverse rows. Mandibles moderately sclerotized, rather long and slender; apex forming a rather long slender tooth which is slightly curved medially and posteriorly; medial teeth near the anterior surface, moderately large and curved posteriorly; posterior and medial surfaces with a few denticles. Maxillae with apex conoidal; palp a slightly elevated disk with three sensilla bearing each a spinule and two encapsulated sensilla; galea subcylindrical with two sensilla on a rounded end. Labium broad and feebly trilobed, with the anterior surface spinulose, the spinules minute and in short transverse rows; between each palp and the opening of the sericteries is an isolated sensillum; palp a low elevation with five sensilla; opening of sericteries a short transverse slit. Dorsal portion of hypopharynx with sublongitudinal ridges; ventral portion spinulose, the spinules minute and in short transverse rows.

Young larva.—Length about 1.3 mm. Both ends bent ventrally at right angles, remainder of body straight; ventral surface of mesothorax, metathorax and first abdominal somite abruptly depressed below the level of the other somites. Hairs somewhat more numerous and a trifle longer than in the mature larva.

Material studied: A dozen larvae from Mt. Poi, Sarawak, Borneo, collected by E. Mjöberg; identified by Dr. W. L. Brown as *V*. sp. near *simoides* Emery.

VOLLENHOVIA OBLONGA PEDESTRIS (F. Smith)

Pl. I, fig. 7

Very similar to *Vollenhovia* sp. but differing in the following details: Body hairs of one type—simple, minute (about 0.001 mm long). Head hairs all simple and minute (about 0.009 mm long). Ventral border of the labrum with a few minute spinules. One of the sensilla on the maxillary palp bears a very long spinule. (***Material studied***: Five damaged integuments from the Solomon Islands.)

HUBERIA Forel

HUBERIA STRIATA (F. Smith)

Emery, 1899: "Il labbro inferiore ha un solo paio di tubercoli conici" (p. 8). Pl. II, Fig. 9, head of larva in side view.

MONOMORIUM Mayr

Athias-Henriot, 1947; Internal anatomy pp. 256, 257, 259, 261, 263, 264, 266, 267.
Gantes, 1949, p. 88: Four sensilla on each maxillary and labial palp.

Subgenus MONOMORIUM Mayr

Plump, chunky and subellipsoidal. Head ventral near the anterior end, on a short stout neck, or neck lacking. Body hairs numerous (or moderately so), uniformly distributed and short; mostly bifid, with long branches, each with a recurved tip; branches frequently denticulate; there may also be a few hairs with bifid tip. Anchor-tipped hairs absent. Head moderately large. Antennae small. Head hairs few, short, bifid, with the branches denticulate; above the antennal level the branches are longer and recurved. Labrum apparently without spinules on the posterior surface. Mandibles of two parts, a stoutly sickle-shaped body and a straight medial blade with several blunt teeth. Maxillary palp a small low knob; galea a short frustum.

MONOMORIUM (MONOMORIUM) PHARAONIS (Linnaeus)

Pl. I, figs. 8-15

Length about 1.9 mm. Plump, chunky and subellipsoidal; diameter greatest at the fourth abdominal somite; ends broadly rounded; dorsal profile C-shaped; ventral profile feebly sinuous. Head on the ventral surface near the anterior end; no neck. Anus posteroventral. Leg vestiges present. Somites indistinct. Spiracles small, the mesothoracic larger than the rest. Integument of the ventral surface of the thorax with a few rows of minute spinules. Body hairs moderately abundant, uniformly distributed and short (about 0.042 mm); bifid, with long branches, each with a recurved tip; branches frequently with a few denticles; rarely much shorter or a little longer or with 3-4 branches; without alveolus and articular membrane (except for a few hairs on the ventral surface). Head moderately large; cranium subtrapezoidal, narrowed ventrally. Antennae small, each with three sensilla, each of which bears a minute spinule. Head hairs few, short (0.027-0.054 mm), bifid (rarely trifid), with denticulate branches; above the antennal level the branches are longer and recurved. Labrum short and broad (breadth 3x the length), ventral border feebly concave; each half of anterior surface with 3-4 hairs with bifid tip; ventral border with four sensilla; each half of posterior surface with two isolated and a cluster of three sensilla. Mandibles moderately sclerotized; of two parts, a stoutly sickle-shaped body and a straight blade projecting medially from the anterior surface; medial border of blade with 2-3 blunt teeth, otherwise variable. Maxillae with the apex paraboloidal; palp a small low knob with four apical sensilla, two of which bear each a rather long spinule; galea a small frustrum with two sensilla, each bearing a rather long spinule. Labial palp a slight elevation with four sensilla, two of which bear a rather long spinule each; an isolated sensillum between each palp and the opening of the sericteries; the latter a moderately long transverse slit.

Very young larva.—Length about 0.41 mm. Plump, fusiform; head ventral, at the anterior end. Body hairs very few, widely scattered, very short (0.006-0.018 mm) and simple. Head hairs few, short (0.009-0.018 mm) and simple.

Young larva.—Length about 0.89 mm. Moderately stout; diameter nearly uniform, greatest at the middle; prothorax inclined ventrally; dorsal profile arched, ventral nearly straight. Integument of dorsal surface of posterior somites sparsely spinulose, the spinules minute and in short rows. Body hairs moderately numerous, uniformly distributed, very short (0.009-0.027 mm), bifid or with denticulate tip. Head hairs few, very short (0.009-0.018 mm), simple or with denticulate tip.

Material studied: Numerous larvae from Panama.

Donisthorpe (1915): "Short and compact, broadest posteriorly, white. *Head* transparent, shining, the rest of the body rugose longitudinally, clothed with short, slightly curved, scattered hairs. The whole larva looks superficially like a bit of broken camphor" (p. 97). Plate II includes a very small and unsatisfactory photograph of a larva in side view. (Repeated 1927, pp. 104-105 and Pl. II.)

MONOMORIUM (MONOMORIUM) FLORICOLA (Jerdon)

Very similar to *pharaonis* but differing in the following details: Integument of dorsal surface of posterior somites also bearing a few rows of minute spinules. Body hairs of two types: 1) a few hairs on the ventral surface of the thorax and first abdominal somite, 0.012-0.036 mm long, with denticulate or bifid tip; 2) elsewhere, deeply bifid, 0.018-0.054

mm long, each branch with the tip recurved; a few branches bear 1-2 denticles. Each half of anterior surface of labrum with 2-3 minute hairs. (*Material studied*: Numerous larvae from Panama.)

MONOMORIUM (MONOMORIUM) MINIMUM (Buckley)

Back, 1937: See below under Marlatt, 1916.

Howard, 1901, fig. 22: A small crude figure of a larva in side view.

Marlatt, 1898, Fig. 2f on p. 2: A small crude figure of a larva in side view. Repeated in the 1907 revision and in several textbooks.

Marlatt, 1916, Fig. 1f: A good figure of a larva in side view. Fig. 1 is an excellent illustration of all castes and developmental stages of this species, which probably accounts for its being one of the most often repeated of myrmecological illustrations. It appeared not only in the 1930 revision but also in the replacing leaflet (Back, 1937) and its revision (1946). It has been repeated in so many textbooks, etc. that it doesn't seem worth while citing any of them.

MONOMORIUM (MONOMORIUM) sp.

Worker larva.—Length about 1.7 mm. Similar to *pharaonis* but differing in the following particulars: Anterior portion of the prothorax forming a very short stout neck; thorax somewhat less stout than in *pharaonis*. Integument of the dorsal surface of the posterior somites also spinulose. Body hairs more numerous. Of two types: 1) on the ventral surface of the thorax and the first two abdominal somites are a few hairs, 0.027-0.054 mm long, with the tip bifid; 2) elsewhere the hairs are 0.024-0.054 mm long, deeply bifid, with very few denticles on the branches. Cranium subrectangular in anterior view, slightly broader than long. Head hairs more numerous. Labrum with four simple hairs on each half of the anterior surface. Labium with a few coarse isolated spinules on the anterior surface at either side.

Young larva.—Length about 0.88 mm. Body and head hairs with the tip simple, bifid or denticulate. Otherwise as in *pharaonis* of the same size.

Sexual larva.—Length about 2.9 mm. Plump, chunky and turgid. On each lateral surface of each somite from the mesothorax through abdominal somite X there are two conical depressions separated by a transverse ruffled welt. Integument rather densely spinulose, the spinules rather coarse and mostly isolated. Body hairs very few and widely scattered (except rather numerous on the prothorax); minute (about 0.009 mm long), slender, simple. Head hairs few, minute (about 0.009 mm long), simple. Otherwise as in the worker larva.

Material studied: numerous larvae from five North Dakota colonies preserved in our collection and bearing field numbers Davis 52, Goldsberry 10, Schonberger 158, Schonberger 175, Uhlmann 251. These all key to *minimum* but Dr. M. R. Smith has kindly examined number 52 for us and has written us as follows: "At one time almost every small black *Monomorium* in North America was called *minimum*, often erroneously. We shall not know the exact taxonomic status of these ants until someone undertakes a careful revision based on large series (especially females, males, associated with workers) from all parts of the United States."

MONOMORIUM (MONOMORIUM) sp.

Similar to *pharaonis* but differing in the following particulars: Thorax more slender. Body hairs more numerous. Hairs on the anterior surface of labrum minute and simple; ventral border with two isolated sensilla. Labium with a few spinules on the anterior surface. (*Material studied*: Numerous larvae from three colonies in our collection—Oklahoma No. 42, Texas No. 10 and Texas No. 150. Dr. M. R. Smith has kindly examined these for us and written as follows: "Although the worker of 150 keys well to *peninsulatum*, a comparison of its female with that of *peninsulatum* clearly indicates that the ants in 150 are not this form.")

Subgenus NOTOMYRMEX Emery

Abdomen greatly inflated and sac-like; thorax forming a rather stout neck which is arched ventrally. Antennae minute. Head hairs few and long; those above the antennal level with the tip bifid; those below with the tip denticulate. Posterior surface of labrum sparsely spinulose, the spinules rather coarse and isolated. Mandibles of two parts, a slender sickle-shaped body and a straight blade projecting medially; medial border of

blade with one or two sharp teeth, otherwise variable. Maxillae with the apex spinulose; palp a short frustum; galea a short subcylinder.

MONOMORIUM (NOTOMYRMEX) ANTARCTICUM (F. Smith)
Pl. I, figs. 16-21

Length about 3 mm. Abdomen greatly inflated and sac-like; thorax forming a rather stout neck which is strongly arched ventrally. Anus ventral. Leg, wing and gonopod vestiges present. Spiracles small, the first pair larger than the rest. Segmentation distinct only on the thorax. Integument with a few short rows of minute spinules on the ventral surface of the thorax. Cranium subtrapezoidal, narrowed ventrally; breadth equal to length; all corners rounded. Antennae minute, each with three sensilla each of which bears a minute spinule. Head hairs few, long (0.027-0.09 mm), those above the antennal level with the tip bifid, those below with the tip denticulate. Labrum distinctly bilobed; breadth 2x the length; lateral borders sinuate, ventral border impressed at the middle; anterior surface of each half with 5-6 minute hairs and/or sensilla; ventral border of each half with two sensilla and a few spinules; posterior surface of each half with 3-4 isolated and a cluster of 2-3 sensilla; posterior surface sparsely spinulose, the spinules rather coarse and isolated. Mandibles moderately sclerotized; of two parts, a slender sickle-shaped body and a straight blade projecting medially; medial border of blade with 1-2 sharp teeth, otherwise variable. Maxillae with the apex paraboloidal and spinulose, the spinules minute and in short subtransverse rows; palp a short frustum with one subapical and four apical sensilla; galea a short subcylinder with two sensilla. Labium with a sparse covering of spinules on the anterior surface; each palp a slight elevation with five sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a moderately long transverse slit.

Young larva.—Length about 1.2 mm. Shape similar to that of mature larva, except that the abdomen is less swollen and its ventral profile is nearly straight. Body hairs long and moderately numerous. Of three types: 1) 0.054-0.13 mm, bifid, with flexible shaft and long flexible branches, the tip of each branch with a single or double hook, the most abundant type; 2) a few anchor-tipped, with tortuous shaft, about 0.13 mm long, on the dorsal surface; 3) a few nearly straight with denticulate tip, 0.027-0.13 mm long, on the ventral surface of the thorax and abdominal somites I-IV.

Material studied: Numerous larvae from New Zealand; all the hairs have been broken off the mature larvae.

Subgenus PARHOLCOMYRMEX Emery

MONOMORIUM (PARHOLCOMYRMEX) GRACILLIMUM (F. Smith)

Gantes, 1949: "☿ 2 mm. 2. Ces larves sont petites, 2 mm. 25 chez l'adulte. Le corps a toujours le même aspect, avec la tête aplatie sur le ventre. Tout autour de la tête, le prothorax est garni d'une couronne de poils longs et simples, rigides: ce sont des poils 'défensifs' de 0 mm. 10. Sur le corps on trouve des poils bifurqués de 0 mm. 040 dont l'extrémité souple des branches s'enroule en crosse ou bien se bifurque. Des poils simples ou fourchus de 0 mm. 05 de long, sont plantés très serrés sous la tête et sur le prothorax. La tête, toujours pyriforme, porte vingt-deux poils, simples ou fourchus. Le labre court, à deux lobes, couvre à peine les mandibules; ventralement on voit une sensille et, sur le dos, trois petits poils. Les mandibules ont la forme de celles de *Pheidole* et mesurent 0 mm. 069. Les palpes maxillaires sont de petits cônes. Le palpe proximal n'a que quatre sensilles dont les soies sont longues et pointues: un sensille est sans soie" (pp. 82-83). Pl. V, fig. VII, larva in side view; Pl. VI, fig. 7 includes mandible, labrum, maxillary palp and galea. Growth, pp. 86 and 87.

Subgenus XEROMYRMEX Emery

Body hairs few, short, variable; simple or branched, mostly two-branched, the main branches smooth or with secondary branches; anchor-tipped hairs absent. Cranium subrectangular in anterior view. Antennae minute, each with 2-4 (usually 3) sensilla. Head hairs few, short, varied in number, location and shape; simple or with the tip denticulate, bifid or trifid. Posterior surface of labrum apparently without spinules. Mandibles of two parts, a stoutly sickle-shaped body and a straight blade projecting medially from the anterior surface; medial border of blade with two distinct teeth, the distal subequal to the

apical tooth, the proximal much smaller. Maxillary palp a small low knob; galea a short frustum.

MONOMORIUM (XEROMYRMEX) AFRUM Ern. André

Pl. I, figs. 22-25

Integument with long rows of minute spinules in a large patch on the ventral surface of the thorax. Body hairs sparse, short (0.036-0.072 mm); variable, simple or branched, mostly 2-branched, the main branches smooth or with secondary branches; with alveolus and articular membrane. Cranium subrectangular, but with the corners rounded. Antennae minute, each with 2-4 sensilla (usually three), each of which bears a short spinule. Head hairs few, short (0.036-0.072 mm), varied in number, location and shape; simple or with the tip denticulate or bifid or trifid. Labrum with the ventral border feebly concave, ventral corners rounded, lateral borders sinuate; breadth 2x the length; anterior surface of each half with two minute hairs and 1-2 sensilla; ventral border of each half with one isolated and two contiguous sensilla; posterior surface of each half with two isolated and two contiguous sensilla. Mandibles heavily sclerotized; of two parts, a stoutly sickle-shaped body and a straight blade projecting medially from the anterior surface; medial border of blade with two distinct teeth, the distal subequal to the apical tooth, the proximal much smaller. Maxillae with the apex paraboloidal; palp a small low knob with four apical sensilla, two of which bear each a rather long spinule; galea a small frustrum with two sensilla. Labial palp a slight elevation with four sensilla, two of which bear a rather long spinule each; an isolated sensillum between each palp and the opening of the sericteries; the latter a moderately long transverse slit. (*Material studied*: Several damaged larvae from the Congo; the specimens are labelled var. *fultor* Forel.)

MONOMORIUM (XEROMYRMEX) SALOMONIS (Linnaeus)

Athias-Henriot, 1947: internal anatomy, pp. 260 and 264; of subspecies *subopacum* pp. 260, 264, and 266 and Fig. 2 on p. 255.

Bernard, 1948: "D'ailleurs, un autre phénomène doit intervenir pour la protection des larves: leur vitesse de transport par les ouvrières en cas de vent de sable, inondation ou autre variation nuisible. J'ai souvent noté la rapidité extrême avec laquelle *Monomorium Salomonis* cachait ses larves une fois le nid ouvert. Il n'en est pas de même pour d'autres espèces, dont les larves ont peut-être alors davantage besoin d'organes bien adaptés?" (p. 107). Internal anatomy, p. 107.

Gantes, 1949: "Ressemble beaucoup à [*gracillimum*]. On note cependant quelques différences: les poils du corps qui sont du même type sont plus longs, 0 mm. 050. Ceux du tour de tête sont plus courts: 0 mm. 069. Les mandibules, de même forme, sont plus grandes, 0 mm. 11" (p. 83). Pl. V, fig. VIII, larva in side view; Pl. VI, fig. 8, mandible, maxillary palp and galea.

MONOMORIUM (XEROMYRMEX) SALOMONIS INDICUM Forel

Dutt, 1912, pp. 251-252: "One morning (3rd July 1909) I observed the inmates of a nest marching out with young ones. Close to the nest was sitting a Muscid fly (*Ochromyia* sp.) which attacked from time to time the larvae and pupae that were being carried by the workers. The fly never snatched the victim from the grasp of the ant, but simply 'licked' it from its place with the proboscis, which when withdrawn left the larva or pupa quite shrivelled up." (Quoted by Wheeler, 1928, p. 256 and in French 1926, p. 309.)

ALLOMERUS Mayr

Comparatively slender; prothorax forming a short thick neck perpendicular to the rest of the body, which is subcylindrical, nearly straight and slightly attenuated to the round-pointed posterior end. Body hairs few, short, uniformly distributed, with the tip denticulate; extremely varied; most are sharply curved near the middle; anchor-tipped hairs absent. Head hairs few, short; angulate or curved; with the distal half denticulate. Labrum small, trilobed; most of the posterior surface densely spinulose, the spinules minute and in numerous subtransverse rows. Mandibles small and short, with the distal fourth strongly bent medially to form a long stout round-pointed apical tooth; apparently without denticles, spinules or medial teeth. Maxillae prominent and appearing adnate to the labium; palp a low elevation; galea a small short knob. Labium prominent and adnate to gula; a small median patch of minute spinules on the anterior surface; palp a slightly raised cluster

of five sensilla. Dorsal portion of hypopharynx with a few longitudinal ridges, the ventral with a few rows of minute spinules.

Sexual larva.—Short, very stout, plump, bean-shaped, curved ventrally; ends large, subequal and broadly rounded; head ventral near the anterior end; no neck. Body mostly naked. Hairs of four types: Type I—extremely long; base stout, straight and heavily sclerotized; attenuating rather rapidly to a slender apical portion, which is slightly curved anteriorly; distal ⅔ denticulate; restricted to posterior ¾ of the ventral surface and arranged in four longitudinal rows. Type II—a few moderately long slender hairs, with the distal half denticulate; curved ventrally; restricted to a small area at the posterior end, dorsal to the anus. Type III—a single pair of moderately long simple slender strongly curved hairs, at the anterior end, one a short distance in front of each mesothoracic spiracle. Type IV—a few minute simple hairs, on the prothorax near the head.

ALLOMERUS DECEMARTICULATUS OCTOARTICULATUS Wheeler

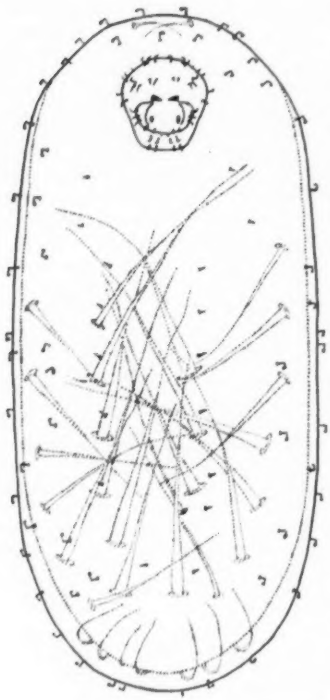
Pl. II, figs. 1-21 and text fig. 1

Mature worker larva.—Length about 1.67 mm. Comparatively slender. Prothorax forming a short thick neck perpendicular to the rest of the body, which is subcylindrical, nearly straight and slightly attenuated to the round-pointed posterior end. Anus terminal. Leg vestiges indistinct. Somites indistinct. Spiracles small, the mesothoracic largest, the others diminishing gradually toward the posterior end. Integument thin, with minute spinules in short transverse rows on the ventral surface of the thorax and the dorsal surface of the posterior abdominal somites. Body hairs few, short (0.009-0.072 mm), uniformly distributed and arranged (at least on the abdomen) in a row around the middle of each somite; tip denticulate; extremely variable; most hairs sharply curved near the middle; usually slenderest and straightest toward the posterior end of the body, longest on the dorsal surface. Head moderately large, subpyriform in anterior view. Antennae rather large with three (rarely two) sensilla, each of which bears a short spinule. Head hairs few and short (0.012-0.018 mm); angulate or curved, with apical half denticulate. Labrum small, width about 2x the length; trilobed, the middle lobe more prominent; anterior surface of each lateral lobe with 1-2 short hairs and 2-3 sensilla; ventral border of each lateral lobe with two isolated and two contiguous sensilla; posterior surface of each half with two isolated sensilla and a cluster of 3-4 sensilla; most of posterior surface densely spinulose, the spinules minute and in numerous subtransverse rows. Mandibles small and rather feebly sclerotized, short, with the distal fourth strongly bent medially to form a long stout round-pointed apical tooth; apparently without denticles, spinules or medial teeth. Maxillae prominent and appearing adnate to the labium; palp a low elevation with five sensilla, three bearing a spinule each; galea a small short knob bearing two sensilla, with a spinule each. Labium prominent and adnate to gula; a small median patch of minute spinules on the anterior surface; palp a slightly raised cluster of five sensilla, three bearing a spinule each; a minute sensillum between each palp and the opening of the sericteries; the latter a short curved transverse slit. Dorsal part of hypopharynx with a few longitudinal ridges, ventral part with a few minute spinules.

Young worker larva.—Length about 1.0 mm. Similar to mature worker larva but more slender.

Sexual larva.—Half-grown (?). Length about 2.35 mm. Short, very stout, plump, bean-shaped, curved ventrally; ends large, subequal and broadly rounded; dorsal profile C-shaped, ventral sinuate; diameter greatest at the middle, decreasing slightly toward each end. Head ventral near the anterior end; no neck. Anus terminal. Somites indistinct. Body mostly naked. Hairs of four types: Type I—extremely long (0.4-0.6 mm); base stout, straight and heavily sclerotized; attenuating rather rapidly to a slender apical portion, which is slightly curved anteriorly; distal ⅔ denticulate; restricted to posterior ¾ of the ventral surface and arranged in four longitudinal rows, 5-8 in each outer row and 4-6 in each inner row. Type II—a few (about 10) moderately long (0.17-0.25 mm) slender hairs, with the distal half denticulate; curved ventrally; restricted to a small area at the posterior end, dorsal to the anus. Type III—a single pair of simple slender strongly curved hairs, about 0.15 mm long, at the anterior end, one a short distance in front of each mesothoracic spiracle. Type IV—a few minute (about 0.009 mm long) simple hairs, on the prothorax near the head. Head and mouth parts like those of mature worker larva.

Young sexual (?) larva.—Length about 1.5 mm. Differs from the mature worker



Text fig. 1.—*Allomerus decemarticulatus octoarticulatus* Wheeler. Larva ready to molt to definitive sexual form; the hairs of the latter are easily seen through the transparent integument of the younger form. Ventral view. × 68.

larva of the same size only in being stouter and in having the abdomen enlarged at the middle, so that the dorsal profile is more convex.

Material studied: numerous larvae from British Guiana, labelled var. *demararae* Wheeler.

The mature worker larva and the older sexual larva are so very different that they might be regarded as belonging to different genera (at the very least). That such is not the case is shown by the fact that we have found young sexual larvae still encased in a worker-like integument (Text fig. 1). Furthermore, a worker pupa enclosed in a worker-larval integument shows that worker larvae do not attain the definitive sexual form before pupating.

In spite of the fact that all larvae of *Allomerus* are alike in the early instars, nevertheless, some slight differentiation does occur previous to the molt to the definitive form. The bodies of small (i.e., worker) semipupae are still about as slender and subcylindrical as are those of most of the young larvae. We have found, however, a few of the size of mature worker larvae, which differ from the latter only in being stouter, and these we have designated as "young sexual (?)" forms.

The descriptions and figures for this species are revised from those of G. C. Wheeler (1935).

MEGALOMYRMEX Forel

Stout; slightly constricted at the first abdominal somite; prothorax stout and turned ventrally at right angles. Body hairs sparse, more numerous and more conspicuous anteriorly and dorsally; ventral and lateral surfaces of abdomen practically naked. Of two types: 1) short, with heavy base tapering to a long fine tip, on the dorsal and lateral surfaces; 2) a few simple and exceedingly minute, on the ventral and lateral surfaces. Anchor-tipped hairs absent. Head hairs few, simple and minute. Mandibles small. Maxillary palp a low irregular elevation; galea a short stout frustrum.

MEGALOMYRMEX (CEPOBROTICUS) SYMMETOCHUS Wheeler

Pl. III, figs. 7-11

Stout; slightly constricted at the first abdominal somite; diameter increasing anteriorly to the mesothorax and posteriorly to the fourth and fifth abdominal somites, then decreasing gradually to VII and thence rapidly to X, which is quite small and directed posteroventrally; prothorax stout and turned ventrally at a right angle; rest of body slightly curved ventrally; anterior end formed from the dorsa of prothorax and mesothorax; posterior end rounded; lateral longitudinal welts present. Anus terminal. Leg vestiges present. Segmentation distinct. Spiracles small. Integument of ventral surface of thorax and first abdominal somite and of dorsal surface of several posterior somites sparsely beset with

minute spinules. Body hairs sparse, more numerous and more conspicuous anteriorly and dorsally; ventral and lateral surfaces of abdomen practically naked. Hairs of two types: 1) with heavy base tapering to a long fine tip, 0.036-0.14 mm long, on the dorsal and lateral surfaces; 2) a few simple and exceedingly minute (0.001-0.009 mm long), on the ventral and lateral surfaces. Cranium subhexagonal in anterior view, slightly broader than long. Antennae drumlin-shaped, each with three sensilla, each of which bears a spinule. Head hairs few, simple and minute (about 0.004 mm long). Labrum short (breadth 2 × length); bilobed; anterior surface of each lobe with four sensilla; ventral border of each lobe with three sensilla; posterior surface of each lobe with a cluster of 2-3 sensilla and five isolated sensilla; posterior surface sparsely spinulose, the spinules minute and isolated or in very short rows. Mandibles small and moderately sclerotized; subtriangular in both anterior and lateral views; apical tooth rather slender and curved medially; a medial blade arises from the anterior surface and bears two subapical teeth and a denticle on the medial border. Maxillae large and prominent; apex paraboloidal; palp a low irregular elevation with three sensilla (bearing a spinule each) and two encapsulated sensilla; galea a short stout frustrum bearing two apical sensilla. Labium with the anterior surface sparsely spinulose, the spinules exceedingly minute and in short transverse rows; palp a low irregular elevation bearing four sensilla; a minute sensillum between each palp and the opening of the sericteries; the latter a transverse slit on the anterior surface. (*Material studied*: Numerous larvae from the Panama Canal Zone.)

This species is a guest-ant of the fungus-growing ant, *Sericomyrmex amabilis* Wheeler. Wheeler (1925, p. 162) observed that "the guest ants kept their brood in small clusters scattered through the garden and each cluster was cared for by a few workers. Although the ants and their brood were thus intermingled, the workers of each species lavished their attention exclusively on their own eggs, larvae and pupae and were never seen even to transport the progeny of the other species from one part of the garden to another." (Quoted by G. C. Wheeler, 1948, p. 673).

"The larvae and pupae of the *Cepobroticus* can readily be distinguished from the *Sericomyrmex* brood. The larvae are more slender and more cylindrical and have smaller heads, with flat, 3-toothed mandibles. The hairs on the body are more numerous, shorter and stouter, though rapidly tapering at their tips. [Quoted by G. C. Wheeler, 1948, p. 673.] I was unable to determine whether the larvae are nourished by regurgitation or feed directly on the fungus hyphae. The fact that they usually lie in the crypts in small clusters and in less intimate contact with the fungus than the *Sericomyrmex* larvae would seem to indicate that they are fed by their nurses with regurgitated liquids" (Wheeler, 1925, p. 163).

G. C. Wheeler, 1948, fig. 1 on p. 672: D, head in anterior view; E, mandible; F, larva in side view. Compared with similar drawings of the host larva.

LIOMYRMEX Mayr

Thorax and first abdominal somite forming a rather long stout neck, which is curved ventrally; rest of abdomen swollen. Body hairs moderately numerous. Of three types: 1) very short, with the tip denticulate, uniformly distributed; 2) long, denticulate from the tip to about the middle, a few on the prothorax and mesothorax and a few on the ventral surface of the metathorax and the first two abdominal somites; 3) long, anchor-tipped, with slender sinuous shaft and feeble hooks, arranged in a band around the middle of most somites. Head small; cranium subquadrate, with the angles rounded. Head hairs short, with denticulate tip; a naked area just above the clypeus. Anterior surface of labrum spinulose; ventral outline broadly curved. Mandibles long, narrow and curved medially; medial portion thin and blade-like, with 8-11 long sharp denticles on or near the middle third of the medial border; with a rather stout blunt subapical tooth on the medial border. Maxillae large, lobose and spinulose; palp a frustrum; galea digitform. Labium bilobed. Hypopharynx spinulose.

LIOMYRMEX AURIANUS Emery

Pl. III, figs. 1-6

Shaped somewhat like a short-neck gourd; thorax and first abdominal somite forming a rather long stout neck which is slightly curved ventrally; rest of abdomen swollen; diameter greatest at the fifth abdominal somite; posterior end broadly rounded. Anus terminal. Segmentation indistinct. Leg vestiges present. Spiracles small, the mesothoracic the largest, diameter of others decreasing posteriorly. Integument of the posterior abdominal somites and of the ventral surface of the mesothorax and metathorax with a few short transverse rows of minute spinules. Body hairs moderately numerous. Of three types: 1) very short (0.018-0.07 mm), with the tip denticulate, uniformly distributed; 2) long (0.105-0.245 mm), denticulate from the tip to about the middle, a few on the prothorax and mesothorax and a few on the ventral surface of the metathorax and the first two abdominal somites; 3) anchor-tipped, with slender sinuous shaft and feeble hooks, long (0.15-0.32 mm), in a band around the middle of most somites, shorter and fewer posteriorly; the first two types lack alveolus and articular membrane. Head small, cranium subquadrate in anterior view, with the angles rounded. Antennae small, each with three sensilla, each of which bears a spinule. Head hairs rather numerous, short (0.018-0.045 mm), with denticulate tip; a naked area just above the clypeus. Labrum broad ($2\frac{1}{2}\times$ the length), ventral outline broadly rounded; anterior surface with 10 minute sensilla and rather numerous short subtransverse rows of minute spinules; ventral border spinulose, the spinules minute and in transverse rows; posterior surface with 5-6 sensilla; posterior surface spinulose, the spinules minute and mostly in rather long subtransverse rows. Mandibles rather heavily sclerotized, long, narrow and curved medially; medial portion thin and blade-like, with 8-11 long sharp denticles on or near the middle 1/3 of the medial border; with a rather stout blunt subapical tooth on the medial border. Maxillae large and lobose, with numerous minute spinules arranged in rows and a few coarser isolated spinules near the base of palp and galea; palp a frustrum with one subapical (bearing a spinule) and four apical (three papilliform and one with a spinule) sensilla; galea digitiform with two apical sensilla, each bearing a spinule. Labium bilobed; anterior surface with numerous short rows of minute spinules; palp a slight elevation with five sensilla; a minute sensillum between each palp and the opening of the sericteries; the latter a short transverse slit. Hypopharynx with rather numerous short rows of spinules. (*Material studied*: Seven larvae from the Philippine Islands, courtesy of Dr. J. W. Chapman.)

ANERGATES Forel

Stout; slightly constricted at the first and second abdominal somites; thorax very stout and curved ventrally at right angles; abdomen slightly curved ventrally; posterior end broadly rounded. Body hairs sparse, more numerous and more conspicuous anteriorly and dorsally. Of three types: 1) generally distributed, short, dendritic, with stout trunk and dense compact branching, the tips of the branches converging; 2) longer denticulate hairs, with the tip simple or branched, a few on the dorsal and lateral surfaces; 3) long anchor-tipped hairs, with tortuous shaft, on the dorsum of abdominal somites I-IV (or I-V). Cranium subhexagonal with the genae bulging slightly. Labrum small, feebly trilobed; only two sensilla on the posterior surface. Mandibles small; distal third narrowed, slightly turned medially, with the apex broadly rounded; without teeth, denticles or spinules. Palps and galeae are slight elevations. Labium long, prominent and feebly bilobed; a few coarse spinules on each lobe; a few short rows of minute spinules dorsal to the opening of the sericteries.

ANERGATES ATRATULUS (Schenck)

Pl. II, fig. 22-30

Stout; slightly constricted at the first and second abdominal somites; diameter increasing anteriorly to the metathorax and posteriorly to the fifth and sixth abdominal somites, then decreasing to either end; thorax very stout and curved ventrally at right angles; abdomen slightly curved ventrally; posterior end broadly rounded; anterior end formed from the dorsa of the prothorax and mesothorax. Anus posteroventral, with a prominent posterior lip. Leg, wing and gonopod vestiges present. Segmentation indistinct on the posterior half. Spiracles small, the first slightly larger than the rest. Body hairs sparse, more numerous and more conspicuous anteriorly and dorsally. Of three types: 1) generally distributed, short (0.036-0.11 mm), dendritic, with stout trunk and dense compact branch-

ing, the tips of the branches converging; 2) longer (0.135-0.22 mm) denticulate hairs, with the tip simple or branched, a few on the dorsal and lateral surfaces; 3) anchor-tipped hairs, about 0.4 mm long, with tortuous shaft, four in a row across the dorsum of each abdominal somite I-IV, and frequently two such hairs on abdominal somite V; occasionally there are also a few hairs that appear to be intergrades between types 2 and 3. Head moderately large; cranium subhexagonal in anterior view, with the genae bulging slightly. Antennae each with three (rarely two) sensilla, each of which bears a minute spinule. Head practically naked but furnished with a few minute (about 0.004 mm long) hairs. Labrum small, breadth 1⅔× length, feebly trilobed; anterior surface with 6-8 minute hairs and/or sensilla; ventral border of each lateral lobe with 2-3 sensilla; posterior surface with two sensilla and numerous transverse rows (of exceedingly minute spinules?). Mandibles small and feebly sclerotized; distal third narrowed, slightly turned medially, with the apex broadly rounded; without teeth, denticles or spinules. Maxillae with the apex paraboloidal; palp a slight elevation with five sensilla; galea a slight elevation with two sensilla. Labium long, prominent and feebly bilobed; a few coarse spinules on each lobe; a few short rows of minute spinules dorsal to the opening of the sericteries; palp a slight elevation bearing five sensilla; a minute sensillum between each palp and the opening of the sericteries; the latter a short transverse slit. (*Material studied*: Numerous larvae from Switzerland.)

Four larvae of this species from Delaware resemble closely those described above but differ in the following details: Constriction of the body more pronounced. Hairs twice as numerous and much more conspicuous because the dendritic hairs are longer (the denticulate and anchor-tipped hairs, however, are shorter). Integument spinulose on the posterior portion of the abdomen, the spinules minute and in very short rows. Labrum twice as broad as long; its ventral border evenly convex.

These differences are of more than usual interest because of the differences between the adults of the European and American forms of *Anergates*. In 1934 Creighton[4] described as a new species (*A. friedlandi*) a single female taken in New Jersey. In 1950 he reduced the name to a synonym of *atratulus* but added, "there is a very strong probability that it will later prove to be a North American subspecies of that form."

Adlerz, 1886: "The larvae are distinguished by coarse, thick and crowded branched hairs with branches bent together at the ends, which are especially well developed on the ventral surface. On the back and sides are found scattered longer aculeate or short-branched hairs as well as anchor-tipped hairs ["ullhår"] with very long double barbs at the end" (p. 274). "*Anergates* larvae have very characteristic coarse hairs which are compactly branched, with the branches crowded together at the ends" (pp. 51-52). Some hairs are deeply forked (p. 268). (Translations from the Swedish by Professor Edith Larson.) Pl. VII, Fig. 5, long denticulate hair; Fig. 5a, short tree-like hair from the dorsal surface. Internal anatomy, p. 58.

Donisthorpe, 1915: "Yellowish white; when young, hairy; more narrow anteriorly than posteriorly; when older, less hairy and nearly as broad anteriorly as posteriorly, but somewhat attenuate in the middle; head naked; the first four somites of the abdomen furnished with long anchor-tipped hairs; the whole body clothed with both long serrate hairs, and short densely and compactly branching hairs" (p. 89). Pl. II includes a small photograph of a larva in side view (Repeated 1927, p. 96 and Pl. II).

Escherich (1906, Fig. 32 = 1917, Fig. 38) repeated Adlerz's figures.

Hölldobler, 1928, p. 142: "Eine *Anergates-Tetramorium-cespitum*-Kolonie nahm den Keulen-Käfer [*Claviger testaceus*] auch gerne auf, aber hier zeigte er sich als verheerender Bruträuber, der alle Tage eine Larve oder Puppe auffrass."

Wheeler (1909, pp. 181-183) stated that the larvae were of a peculiar gray color, that those in a colony were all of the same size and uniformly developed and that they adhered to the lower surface of the stone that covered the nest by means of their hooked dorsal hairs. "I give a figure (Fig. 2*A*) of a larva . . . and also of a mature worker larva of *Tetramorium* (Fig. 2*B*) for comparison. It will be seen that though both larvae possess pairs of long anchor-tipped dorsal hairs, the head of the *Anergates* larva is naked, and its short dorsal and ventral hairs (*b*) are much more densely and compactly branching, while the longer hairs (*a*) are serrate are not branched at their tips like the homologous structures (*d*) of the *Tetramorium* larva. The anchor-tipped hairs (*c*) with sigmoid basal

[4] Bull. Mus. Comp. Zool. Harvard Coll. 104:241-242. 1950.

flexure are used in both species for fastening the larvae to the lower surfaces of stones, the roots of plants and the walls of the galleries and chambers of the nest."

ANERGATIDES Wasmann

Elongate-subellipsoidal, with the head on the anterior end. Body hairs moderately numerous and uniformly distributed. Of two types; 1) short, dendritic (with open branching); 2) long, anchor-tipped, with tortuous shaft. Head subtriangular in anterior view. Antennae protuberant and drumlin-shaped, with two sensilla each. Head hairs few, short, with bifid tip. Only two sensilla on posterior surface of labrum. Mandibles small, plump, slightly curved medially; apex paraboloidal and surmounted by a single denticle; on the medial surface are a few transverse rows of minute spinules. Palp a small frustrum; galea a short curved protuberance. Anterior surface of labium sparsely spinulose.

ANERGATIDES KOHLI Wasmann

Pl. II, figs. 31-32)

Elongate-subellipsoidal, with the head on the anterior end. Leg and wing vestiges present. Spiracles small. Body hairs moderately numerous and uniformly distributed. Of two types: 1) about 0.1 mm long, dendritic (with open branching), the base stout and slightly curved, the branches acuminate; 2) about 0.25 long, anchor-tipped, with tortuous shaft. Head subtriangular in anterior view; cranium subpentagonal, breadth nearly twice the length, narrowed ventrally, with the occipital corners rounded. Antennae protuberant, drumlin-shaped; each with two sensilla, each of which bears a spinule. Head hairs few, short (about 0.02 mm), with bifid tip. Labrum subtrapezoidal, narrowed ventrally; breadth twice the length; anterior surface with four minute hairs; ventral border with two sensilla; ventral and lateral surfaces with a few spinules; posterior surface with two sensilla and with minute spinules arranged in numerous, long subtransverse rows. Inside the labrum is a heavily sclerotized triangular structure, with the base of the triangle along the ventral border of the labrum. Mandibles small and heavily sclerotized, plump, slightly curved medially, apex paraboloidal and surmounted by a single small denticle; on the medial surface are a few transverse rows of minute spinules. Maxillae small; palp represented by a small frustrum bearing three sensilla and two contiguous sensilla; galea a short curved protuberance bearing two apical sensilla. Labium with the anterior surface bearing a few subtransverse rows of minute spinules; palp represented by a low elevation bearing three sensilla; on the anterior surface near each palp is a conspicuous hair; opening of the sericteries a rather long transverse slit. (*Material studied*: Two badly damaged larvae from the Belgian Congo. As far as we can learn *Anergatides* has been collected only once, hence these larvae are probably from the type nest. They were probably sent by Wasmann to W. M. Wheeler, who handed them over to G. C. Wheeler for study.)

This is one of the most extraordinary ant larvae we have studied; they are no more remarkable, however, than the adults, which are workerless social parasites of *Pheidole megacephala melancholica* Santschi.

BRUCHOMYRMA Santschi

BRUCHOMYRMA ACUTIDENS Santschi

Bruch, 1931: "Muy semejante a la larva de las mismas *Pheidole* (st. *Strobeli*) en cuanto a forma y pilosidad; pero se distingue de ésta de inmediato, por la visibilidad de los vasos de Malpighi, que se destacan muy nítidamente en el fondo obscuro del tubo digestivo. Su cuerpo es apenas más encorvado; la cabeza apenas más pequeña; la pilosidad bífida es algo más abundante y apenas más gruesa que en las *Pheidole*. Completamente crecidas, las larvas tienen 2,3 a 2,7 milímetros de largo; el tegumento es liso, de brillo aceitoso, la pilosidad amarillenta, pálida está formada por cilias cortas con ganchitos terminales bífidos, apenas encorvadas; también llevan, como las larvas de *Pheidole*, los cuatro pares de pelos dorsales largos, semienroscados en la base (*spring hairs*) y también bífidos en el ápice. Como de costumbre, luego de alcanzado el crecimiento máximo, evacua el tubo digestivo y adquiere entonces un color uniforme amarillento, de aspecto ceroso y de consistencia más dura" (pp. 46-47). Fig. 5 on p. 51, larva in side view. Pl. I, fig 2; Pl. IV; Pl. VI, fig. 2: photographs of larvae.

TRANOPELTA Mayr

Stout; head ventral, near the anterior end. Body hairs rather numerous, uniformly distributed, short and deeply bifid; anchor-tipped hairs absent. Antennae with two sensilla each. Head hairs few, short and deeply bifid. Labrum small and short. Mandibles small, apex curved medially and acuminate; with one small medial tooth, or none. Maxillary palp a low knob; galea a frustum.

TRANOPELTA GILVA Mayr

Pl. III, figs. 12 and 13

Length about 2.3 mm. Stout; head ventral, near the anterior end. Leg and wing vestiges present. Spiracles small. Body hairs rather numerous, uniformly distributed, short (about 0.054 mm); deeply bifid, the branches $2/3$ of the total length and strongly divergent; without alveolus or articular membrane. Antennae each with two sensilla, each of which bears a spinule. Head hairs few, short (0.018-0.045 mm), shaped like body hairs but with alveolus and articular membrane. Labrum small and short (breadth 4× the length), subtrapezoidal, narrowed ventrally; anterior surface with eight sensilla; ventral border with two sensilla and a few spinules; posterior surface spinulose, the spinules minute and in numerous subtransverse rows. Mandibles small, moderately sclerotized, subtriangular in anterior view; apex curved medially and acuminate; with one small medial tooth, or none. Maxillary palp a low knob with five sensilla; galea a frustum with two sensilla. Labial palp a low knob; opening of sericteries a short transverse slit. (*Material studied*: Six damaged integuments from British Guiana.)

Young larva.—Length about 1.1 mm. Head and prothorax curved ventrally, abdomen with the ventral profile nearly straight and the dorsal profile strongly curved; diameter greatest at the fourth and fifth abdominal somites. Hairs similar to those of mature larva. (*Material studied*: a dozen larvae from the Panama Canal Zone.)

CAREBARELLA Emery

CAREBARELLA BICOLOR var. PUNCTATO RUGOSA Emery

Eidmann, 1936: "Die riesigen, fast kugeligen Larven der Geschlechtstiere . . . Während die Arbeiterlarven auch in den ältesten Stadien mit einem dichten Pelz tiefgegabelter Haare bedeckt sind, zeigen jene nur eine sehr spärliche Behaarung. Ihre Haut ist glatt gespannt, so dass die Segmentierung verwischt ist, und der weisse, segmental angeordnete Fettkörper schimmert durch die Körperoberfläche hindurch. Sie sind so gross, dass man sich kaum vorstellen kann, dass die kleinen Arbeiter diese riesigen Gebilde fortbewegen können, was wahrscheinlich auch nicht oder nur in beschränktem Masse stattfinden dürfte. In starkem Missverhältnis zu dieser Grösse steht der winzig kleine Kopf, der nicht grösser ist als bei einer Arbeiterlarve" (p. 44). Fig. 2c on p. 43, a mature sexual larva in side view.

SOLENOPSIS Westwood

Stout; prothorax bent ventrally at right angles to form a very short stout neck; rest of body straight; both ends broadly rounded. Body hairs numerous, short, uniformly distributed. Five types of body hairs occur: 1) simple and slightly curved; 2) simple, with the tip sharply recurved; 3) with denticulate tip; 4) with short-bifid tip; 5) deeply bifid, the branches usually perpendicular to the base, the tips recurved. A species usually has two of these types, but some have three. Anchor-tipped hairs absent. Head large and subpyriform. Head hairs few and rather long. Four types occur: 1) simple; 2) with denticulate tip; 3) with short-bifid tip; 4) bifid. Every species has the bifid type and also one or two of the other types. Mandibles of two parts, a stoutly sickle-shaped body and a medial blade, the medial edge of the latter forming several teeth. Maxillary palp peg-like; galea a short frustum. Labium with a patch of spinules dorsal to each palp. *Queen larva* generally similar to worker but more voluminous, with the head and hairs relatively smaller; no neck, the head being applied to the ventral surface near the anterior end. The *immature sexual larva* differs from the mature worker larva of the same length in having the large head on the end of a short stout neck formed from the prothorax, which is inclined ventrally; remainder of body sac-like.

Clausen, 1940, p. 221: The eucharid wasps of the genus *Orasema* appear to be most frequently associated with *Pheidole* and *Solenopsis*. (Eucharid larvae are parasitic on ant larvae.)

Gantes, 1949: Sexual larvae are quite different from worker larvae (p. 88). "La croissance est uniformément faible, à peine plus marquée au stade V" (p. 85).

Stärcke (1948, p. 28) describes the soldier larva as follows: "Body still more swollen, of a short oval or nearly globose shape, with a small head projecting on the ventral side."

SOLENOPSIS (SOLENOPSIS) GEMINATA (Fabricius)

Pl. III, figs. 14-24

Worker larva.—Length about 2.6 mm. Stout; prothorax bent ventrally at right angles to form a very short stout neck; rest of body straight; diameter greatest at the fourth abdominal somite, both ends broadly rounded; dorsal profile curved, ventral profile nearly straight. Anus ventral. Leg and wing vestiges present. Segmentation indistinct. Spiracles small, the first larger than the others. Integument of the ventral surface of the thorax and the first three abdominal somites with a few short transverse rows of minute spinules. Body hairs numerous, short, uniformly distributed. Of two types: 1) simple, slightly curved, 0.054-0.108 mm, with alveolus and articular membrane, 6-12 in a transverse row on the ventral surface of each thoracic somite and on each of the three anterior abdominal somites; 2) elsewhere the hairs are bifid, about 0.07 mm long, the base about half the length, the branches more or less perpendicular to the base, the tips recurved; hairs on the ventral surface with alveolus and articular membrane. Head large, subpyriform in anterior view; cranium slightly broader than long. Antennae each with three sensilla, each of which bears a spinule. Head hairs few; those above the antennal level are moderately long (about 0.054 mm) and bifid; those below are long (0.09-0.126) mm) and simple. Labrum small, short (breadth 2× the length), slightly narrowed dorsally, ventral border feebly concave, ventral corners rounded; anterior surface of each half with five minute sensilla; ventral border with a few coarse isolated spinules; each half of posterior surface with 2-3 isolated and two contiguous sensilla and with a few coarse isolated spinules near each ventrolateral corner. Mandibles heavily sclerotized; of two parts, a stoutly sickle-shaped body and a straight medial blade, the medial edge of the latter forming 2-5 teeth which decrease in size dorsally. Maxillae with the apex conoidal; palp a peg with five sensilla, one of which bears a spinule; galea a short frustrum with two apical sensilla. Labium with a patch of spinules dorsal to each palp, the spinules rather coarse and isolated or in short rows of 2-3; palp a slight elevation with five sensilla, one of which bears a spinule; opening of sericteries a rather long transverse slit.

Soldier larva.—Length about 5.2 mm. Stouter; anterior end more broadly rounded; head relatively smaller, on the ventral surface near the anterior end, i.e., no neck. Integument of the ventral surface of the mesothorax, metathorax and first two abdominal somites with a few spinules. Body hairs longer; all with alveolus and articular membrane. Otherwise similar to worker larva.

Very young larva.—Length 0.63-0.69 mm; probably first instar. Anterior end recurved; head relatively quite large, its diameter almost as great as that of the body which is nearly uniform. Integument of the dorsal surface of posterior somites sparsely spinulose, the spinules minute and in very short subtransverse rows. Body hairs sparse, stout, short (0.006-0.018 mm), longest on the prothorax and ventral surface. Of three types: 1) simple; 2) with the tip curled; 3) with the tip bifid. Head hairs few, short (0.009-0.018 mm) and stout, similar to body hairs. Labrum short (breadth 3× the length); subtrapezoidal, narrowed ventrally; anterior surface with six sensilla; posterior surface with two contiguous sensilla on each half and a few minute spinules near the ventral border. Mandibles feebly sclerotized, short and stout, breadth equal to length; terminating in a small cone; blade represented by a rounded medial projection. Maxillae with the apex paraboloidal; palp a slight elevation with five minute sensilla; galea represented by two sensilla. Labium with the anterior surface sparsely spinulose, the spinules minute and in short subtransverse rows; each palp represented by a cluster of five sensilla, one of which bears a spinule; opening of sericteries a short transverse slit.

Material studied: Numerous larvae from Texas.

Eidmann, 1944, p. 451: "Die Larven fallen durch ihr dick aufgetriebenes Abdomen auf und besitzen einen dichten Pelz ankerförmiger Haare, der sie leicht zusammenballen lässt."

Wheeler (1900, Fig. 10) labelled a drawing as *Solenopsis geminata;* but the same

figure reproduced in 1910 (Fig. 43 on p. 77) was labelled *Pheidole instabilis*. We have this note in Dr. Wheeler's handwriting referring to the 1900 figure: "erroneously described and figured as *Solenopsis geminata!*" Escherich (1906, Fig. 30 and 1917, Fig. 36D) copied Wheeler's figure of the mature larva and labelled it *Solenopsis geminata*.

SOLENOPSIS (SOLENOPSIS) GAYI (Spinola)

Goetsch, 1937, p. 807: Giant forms are produced where the larvae are fed on chewed seeds ("Ameisenbrot"), as in the north of Chile, while in the south where this species uses crop feeding polymorphism practically disappears.

SOLENOPSIS (SOLENOPSIS) SAEVISSIMA (F. Smith)

Wheeler (1928, p. 253 = 1926, p. 305): "Borgmeier has found that the larvae of a Brazilian species [of *Microdon*] actually devours the larvae of its host." But upon examining the reference we find that Borgmeier reported the *Microdon* larvae as feeding on a coccid, not upon ant larvae.

SOLENOPSIS (SOLENOPSIS) XYLONI McCook

Worker larva.—Length about 2.9 mm. Very similar to *geminata* except in the following details: Some of the body hairs of type 1 may have the tip recurved or denticulate; there are intergrades between types 1 and 2. Head moderately large. Bifid head hairs are few, short and restricted to the occipital border; the others have the tip simple or finely denticulate. Near the base of the anterior surface of the labium is a low welt furnished with coarse isolated spinules.

Queen larva.—Length about 5.6 mm. Body voluminous, somewhat stouter posteriorly. Head relatively smaller; on the ventral surface near the anterior end. Otherwise similar to the worker larva.

Material studied: Numerous larvae from Texas.

SOLENOPSIS (DIPLORHOPTRUM) BASALIS Forel

Eidmann, 1936, p. 45: "Die Larven sind dicht behaart mit tief gegabelten Acrochaeten, deren Enden hakenförmig gekrümmt sind, und die überragt werden von sehr zahlreichen Oncochaeten, die in eine einfache gekrümmte, oft geradezu eingerollte Spitze auslaufen."

SOLENOPSIS (DIPLORHOPTRUM) FUGAX (Latreille)

The body hairs are slightly longer, and the hairs on the ventral surface of the thorax may have either simple or denticulate tip. Anterior surface of the labium apparently without spinules. Otherwise the larvae of this species seem to be similar to *molesta*. (*Material studied*: 16 damaged larvae from Japan and Switzerland.)

Donisthorpe, 1915: "Pyriform, though somewhat narrowed at the extreme base, covered with short curved hairs. The smaller larvae (☿) are yellow, smooth and shining, the larger ones (♂ ♀?) are white, duller and more rugose" (p. 103). Pl. I includes small photographs of larvae in side view. (Repeated 1927, p. 111 and Pl. I.)

Forel, 1874: "Très courtes, épaisses aux deux bouts, raides et indistinctement annelées. . . . Extrêmement raides, presque incapables de remuer même leur tête" (p. 388). In the 1920 edition (p. 265) the first sentence reads: "Très courtes, épaisses aux deux bouts, entièrement raides"; the second sentence (p. 266) is unchanged. "Certaines larves, sorties de l'oeuf en automne, ne deviennent nymphes qu'au mois de juillet de l'année suivante" (p. 389; =1920, p. 266; cited by Adlerz, 1886, p. 53).

Gösswald (1929, p. 204) recorded *Mermis*-like larvae in the larvae of this ant. In 1930 he reported finding larvae of this ant parasitized by *Mermis* (Nematoda). (Cited by Vandel, 1930, p. 470.) In 1934-35 he cited (p. 125) it as a mermithid host.

Hölldobler (1927) has reported two larvae of this ant as parasitized by something.

Hölldobler, 1928, pp. 136-137: "In den anderen Nestern begann die Eiablage Ende Mai. Nach etwa 16 Tagen zeigten sich die ersten Larven. Diese pflegten zu überwintern, stiessen dann Ende Mai des nächsten Jahres den Kotsack aus, verpuppten sich Anfang Juni, und Mitte Juli hatte ich die ersten jungen Ameisen. Larven die noch in Spätherbst (November) den Kotsack ausstiessen, sich also zur Verpuppung rüsteten, wurden regel-

mässig von den Ameisen gefressen. Die Bruthäufchen sind sehr sauber geschichtet. Zu unterst liegen die grossen Larven, dann die Puppen und die vor der Verpuppung stehenden Larven, zu oberst liegt die Jungbrut. Auch die Fähigkeit, feste Nahrung aufzunehmen, beobachtete ich an Diebsameisenlarven. Als ich meine Nester schlecht fütterte, hatten zahlreiche Larven kleine weisse Stückchen vor der Mundöffnung, die ich als Reste eigenen Brut erkannte. Diebsameisen griffen in schlechten Zeiten häufig den eigenen Larvenbestand an."

SOLENOPSIS (DIPLORHOPTRUM) MOLESTA (Say)

Pl. III, figs. 25-27

Worker larva.—Length about 1.5 mm. Generally similar to *geminata* except in the following details: Mesothoracic spiracle the largest; metathoracic and first abdominal nearly as large; the others only half as large. Integument of ventral surface of thorax furnished with rather coarse spinules arranged in moderately long transverse rows; there are also a few scattered spinules on the dorsal surface of the posterior somites. Body hairs relatively shorter; type 1—0.018-0.045 mm long; type 2—0.018-0.036 mm long; type 1 hairs all have denticulate tip; intergrades between the two types occur where their ranges meet; some of the intergrades have alveolus and articular membrane, which all other body hairs lack. Head moderately large. The longer head hairs may have the tips either simple or denticulate. No spinules on the posterior surface of the labrum. The teeth on the blade of the mandible highly variable. Anterior surface of the labium sparsely spinulose, the spinules isolated or in very short rows.

Very young larva.—Length about 0.54 mm. Head relatively very large. Head and prothorax inclined ventrally. Abdomen somewhat slenderer than in the mature larva. Integument of dorsal surface spinulose, the spinules minute and in short transverse rows. Body hairs simple, minute (0.006-0.012 mm long), restricted to about ten longitudinal rows, apparently without alveolus and articular membrane. Head hairs simple and minute (0.006-0.009 mm long).

Young larva.—Length about 0.83 mm. Head relatively larger and abdomen slenderer than in the mature larva. Body curved ventrally. Integument of the dorsal surface of the posterior somites spinulose, the spinules minute and isolated or in very short transverse rows. Body hairs moderately numerous, uniformly distributed, minute (0.006-0.018 mm long), mostly with long shaft and short bifid tip, without alveolus and articular membrane. Head hairs short (0.012-0.018 mm), with the tip bifid.

Queen larva.—Length about 3.5 mm. Voluminous; head relatively very small, on the ventral surface near the anterior end; dorsal profile C-shaped. Anus ventral. Body hairs very scarce and relatively very short, with alveolus and articular membrane; body practically naked except for the prothorax, mesothorax and the dorsal surface of the remaining somites. Of two types: 1) simple, 0.018-0.054 mm long, on the prothorax and mesothorax; 2) about 0.036 long, bifid, with short base and long flexible branches, limited to the dorsal surface. Otherwise similar to the worker larva.

Immature sexual larva.—Length 1.4-1.7 mm. Head large, on the end of a short stout neck formed from the prothorax, which is inclined ventrally; remainder of body saclike; dorsal profile C-shaped; ventral profile nearly straight. Anus ventral. Integument of ventral surface of prothorax and mesothorax with a few coarse spinules in very short transverse rows; a few isolated spinules on the metathorax; the dorsal surface of the posterior somites sparsely spinulose, the spinules minute and mostly isolated. Body hairs numerous, short, uniformly distributed, all with alveolus and articular membrane. Of three types: 1) about eight relatively long (0.036-0.063 mm), stout hairs with the tip simple or denticulate, on the ventral and lateral surfaces of the prothorax; 2) on the ventral surface of mesothorax, metathorax and first abdominal somite are a few shorter (0.027-0.045 mm), bifid hairs, with base and branches about equal in length; 3) elsewhere the hairs are about 0.018 mm long and deeply bifid. Otherwise similar to the worker larva.

Material studied: Numerous larvae from Arkansas, Connecticut, North Dakota, Oklahoma and Texas.

Hayes, 1920: "The larvae of this species resemble superficially the larvae of any of the other Myrmicine ants except, perhaps, in size. They are white in color and covered with double-hooked hairs which enable them to cohere in packets and so be carried by the workers. The posterior end is large and tapers toward the anterior end, which is considerably curved. This curvature becomes less pronounced as the larva grows older, but

is never entirely obliterated. When first hatched the young larvae are scarcely larger than the eggs from whence they came. The length of the larval stage is highly variable, depending on weather conditions to a marked degree. During midsummer, larvae were reared to the semipupal stage in 21 days. In another instance, a single larva was under observation from October 10 to May 12 when it transformed to the semipupal stage. Larvae are fed regurgitated food by the workers. Workers, in artificial nests, were often seen to place small bits of crushed kafir seeds and torn parts of their larvae and pupae on the bodies of the young near the mouthparts where the larvae were seen to bite them. Larvae were frequently observed, while lying on their back, to straighten out their curved body. These movements are repeated at short intervals and the mandibles open at each up-movement and close on the down-movement. These moving larvae were generally fed at once, or soon after making these apparent supplications. As the larva becomes full grown, a large undigested meconium is voided from the alimentary tract. Workers were seen at times aiding the larva to get rid of this mass by tugging at it while it was being cast off. This change marks the end of larval development and the beginning of the semipupal stage. Large larvae have often been encountered in nests of this species, which were, undoubtedly, either larvae of males or queens. . . . Except for their much greater size, they resemble the worker larvae, and upon reaching their final stages of growth undergo similar changes to the semipupal stage. In this stage, they are not greatly unlike the larvae except for the absence of the black mass in the abdomen. The semipupal stage was found in midsummer to vary from 2 to 11 days" (pp. 31-32). Fig. 7, a worker larva in side view.

McColloch & Hayes, 1916, pp. 28-29: Quoted almost verbatim by Hayes, 1920 (see above). Pl. 2, fig. 2, photograph of five worker larvae at different stages of growth.

SOLENOPSIS (DIPLORHOPTRUM) MOLESTA VALIDIUSCULA Emery

Scarcely distinguishable from *molesta*. The body hairs of this form are slightly longer and the posterior surface of the labrum bears a few spinules on or near each ventrolateral corner. *Material studied*: a dozen larvae from Colorado.

Wheeler (1907, p. 12) recorded the eucharid wasp *Orasema coloradensis* Ashmead from the nest of this ant. Presumably the wasp larva had been parasitic on an ant larva.

SOLENOPSIS (DIPLORHOPTRUM) PICEA Emery

Pl. III, figs. 28-31

Length about 1.4 mm. Body hairs of three types: 1) on the dorsal surface of the thorax are a few hairs 0.045-0.063 mm, with sharply recurved tip; 2) on the ventral surface of the thorax, 0.027-0.036 mm, with long base and denticulate or short-bifid tip; 3) elsewhere bifid, 0.027-0.054 mm, with short base and long flexible branches. The larger head hairs may have either denticulate or short-bifid tips. Each antennal sensillum bears a relatively long flexible hair. Each maxillary and labial palp with four sensilla, two of which bear a spinule each. Otherwise similar to *molesta*.

Very young larva.—Length about 0.64 mm. Slender; diameter nearly uniform throughout; head on the anterior end, which is curved ventrally. Body hairs numerous and uniformly distributed, simple, with the tip recurved, 0.009-0.027 mm; on the prothorax a few hairs are about 0.018 mm long and have a short-bifid tip. Head hairs 0.009-0.027 mm long, with the tip recurved; a very few have the tip bifid.

Young larva.—Length about 0.8 mm. Body shape similar to that of the younger larva; otherwise similar to the mature larva.

Material studied: Numerous larvae from Costa Rica.

SOLENOPSIS (DIPLORHOPTRUM) SCHMALZI Forel

Eidmann, 1936, p. 46: "Die Larven waren von einem dichten Pelz grosser, gegabelter Haare bedeckt."

SOLENOPSIS (DIPLORHOPTRUM) TENUIS Mayr

Length about 1.6 mm. Body hairs of three types: 1) a few 0.036-0.054 mm long, simple with flexible shaft and recurved tip, on the dorsum of the thorax; 2) on the venter of the thorax are a few hairs 0.036-0.045 mm long, simple, with flexible shaft; 3) elsewhere bifid, 0.018-0.036 mm long. Head hairs of two types: 1) mostly bifid, 0.027-0.036 mm long, with short trunk and flexible branches; 2) a few on the ventral part of the

cranium are simple and about 0.027 mm long. Each maxillary and labial palp with four sensilla, one of which bears a rather long spinule. Labium apparently without spinules. Otherwise similar to *molesta.*

Young larva.—Length about 0.71 mm. Head and thorax bent ventrally, rest of body curved ventrally. Anus ventral. Mouth parts directed posteriorly. Body hairs numerous, short (0.006-0.018 mm), stout, with the tip recurved.

Next instar.—Length about 0.75 mm. Body hairs of three types: 1) most of the hairs on the dorsal surface of the prothorax and mesothorax simple, with flexible shaft and recurved tip, 0.054-0.063 mm long, shorter and sparser on the rest of the dorsal surface. 2) on the ventral surface of the thorax and first abdominal somite are a few hairs 0.018-0.045 mm long, with curved shaft and simple or denticulate tip; 3) elsewhere bifid and 0.036-0.045 mm long. Otherwise similar to mature larva.

Material studied: 14 specimens from Costa Rica.

G. C. & E. W. Wheeler (1937) have recorded the larvae of the eucharid *Orasema sixaolae* G. C. & E. W. Wheeler as parasitic in the larvae of this ant. (Referred to by Clausen, 1940, p. 227).

SOLENOPSIS (DIPLORHOPTRUM) TEXANA Emery

Length about 1.6 mm. Scarcely distinguishable from *molesta.* The body hairs of *texana* are somewhat longer, the ventral head hairs have denticulate tips only and the labium is apparently without spinules.

Very young larva.—Length about 0.78 mm. Rather slender, diameter practically uniform throughout. Head and prothorax bent ventrally; rest of body curved ventrally. Anus terminal. Body hairs numerous, short (0.009-0.027 mm), with long shaft and simple recurved or short-bifid tip; without alveolus and articular membrane.

Material studied: 17 larvae from Oklahoma.

SOLENOPSIS (subgenus?) ROBUSTA Bernard

Gantes, 1949: "Le corps a le même aspect que la larve d' ☿ de *Pheidole.* Elle est légèrement plus petite, 1 mm. 75. Les segments sont bien visibles; la première paire de stigmates légèrement plus grande. Tout le corps est couvert de petits poils de 0 mm. 05, qui se divisent en deux branches à la moitié de leur hauteur. Ils sont très souples et leurs extrémités se recourbent en crosse. La tête est bien différenciée, en forme de coeur plutôt que de poire. Elle est couverte de vingt poils simples ou fourchus. Le labre a la forme d'un demi-cercle. Ventralement, en avant et latéralement, nous avons un groupe de quatre sensilles, trois accolées et une à côté. Les mandibules de même forme que les précédentes mesurent 0 mm. 069. Les palpes maxillaires ont des sensilles dont les soies sont longues et aiguës et ont l'air ainsi de petits chapeaux pointus. Le palpe maxillaire est garni de cinq sensilles dont deux plus grosses sans soies. Le palpe labial a cinq sensilles toutes à soies. La larve de sexué n'en diffère que par sa taille" (p. 81). Pl. IV, Fig. IV: Larva in side view, mandible, hairs, maxillary palp and galea. Growth data are to be found on p. 86.

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EXPLANATION OF PLATES

PLATE I.

Vollenhovia sp. Figs. 1-6—1, head in anterior view, ×95; 2, left mandible in anterior view, ×235; 3 and 4, two types of body hairs, ×235; 5, young larva in side view, ×20; 6, larva in side view, ×20.

Vollenhovia oblonga pedestris (F. Smith). Fig. 7.—Right maxillary palp in anterior view, ×432.

Monomorium (*Monomorium*) *pharaonis* (Linnaeus). Figs. 8-15.—8, head in anterior view, ×95; 9, right maxillary palp in anterior view, ×680; 10, left mandible in anterior view, ×185; 11, mature larva in side view, ×32; 12, young larva in side view, ×32; 13, very young larva in side view, ×32; 14 and 15, two types of body hairs, ×370.

Monomorium (*Notomyrmex*) *antarcticum* (F. Smith). Figs. 16-21.—16, head in anterior view, ×86; 17-19, three types of body hairs of young larva, ×185; 20, outline of young larva in side view, ×18; 21, outline of larva in side view, ×18.

Monomorium (*Xeromyrmex*) *afrum fultor* Forel. Figs. 22-25.—22, head in anterior view, ×76; 23, left mandible in anterior view, ×185; 24 and 25, two types of body hairs, ×242.

PLATE II.

Allomerus decemarticulatus octoarticulatus Wheeler. Figs. 1-21.—1, head in anterior view, ×121; 2, left mandible in anterior view, ×433; 3-14, twelve body hairs, ×185; 15, larva in side view, ×45; 16, immature sexual larva in side view, ×33; 17, Type I body hair of sexual larva, ×185; 18, Type III body hair of sexual larva, ×185; 19, Type IV body hair of sexual larva, ×185; 20, Type II body hair of sexual larva, ×185; 21, outline of bodies of mature worker and sexual larvae, ×8.

Anergates atratulus (Schenck) from Switzerland. Figs. 22-30.—22, head in anterior view, ×95; 23, left mandible in anterior view, ×185; 24, left mandible in medial view, ×185; 25, anchor-tipped hair, ×56; 26 and 27, denticulate hairs, ×56; 28, dendritic hair, ×56; 29, dendritic hair further enlarged, ×443; 30, larva in side view, ×20.

Anergatides kohli Wasmann. Figs. 31-32.—31, head in anterior view, ×95; 32, left mandible in anterior view, ×467.

PLATE III.

Liomyrmex aurianus Emery. Figs. 1-6.—1, head in anterior view, ×86; 2, left mandible in anterior view, ×185; 3-5, three types of body hairs, ×95; 6, larva in side view, ×20.

Megalomyrmex (*Cepobroticus*) *symmetochus* Wheeler. Figs. 7-11.—7, head in anterior view, ×86; 8 and 9, two types of body hairs, ×185; 10, left mandible in anterior view, ×235; 11, larva in side view, ×15.

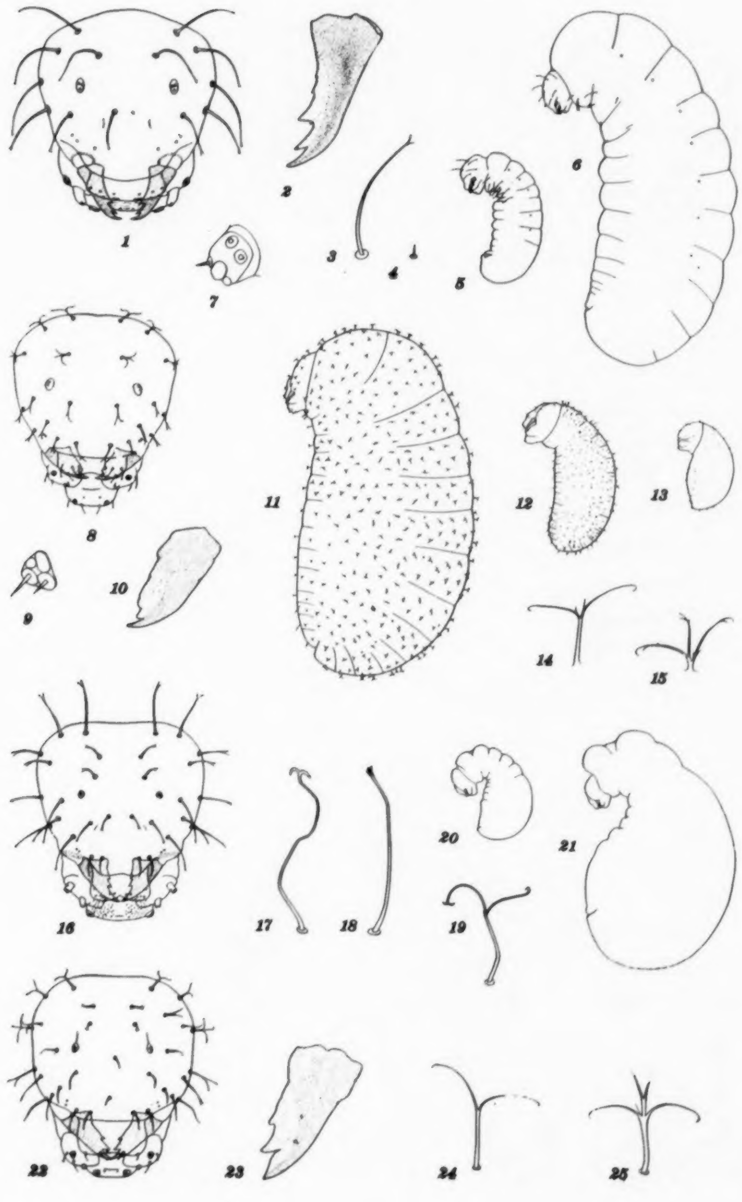
Tranopelta gilva Mayr. Figs. 12 and 13.—12, right mandible in anterior view, ×470; 13, body hair, ×235.

Solenopsis (*Solenopsis*) *geminata* (Fabricius). Figs. 14-24.—14, head in anterior view, ×76; 15, left mandible in anterior view, ×185; 16, left mandible in medial view, ×185; 17 and 18, two types of body hairs, ×235; 19, mature larva in side view, ×20; 20, first (?) instar larva (hairs too small to show), ×20; 21, left mandible of first (?) instar larva in anterior view, ×185; 22-24, three types of body hairs of first (?) instar larva, ×470.

Solenopsis (*Diplorhoptrum*) *molesta* (Say). Figs. 25-27.—25, profile of mature sexual larva, ×10; 26, profile of immature sexual larva, ×10; 27, profile of mature worker larva, ×10.

Solenopsis (*Diplorhoptrum*) *picea* Emery. Figs. 28-30.—28, left antenna in anterior view, ×428; 29-31, three types of body hairs, ×235.

PLATE I.



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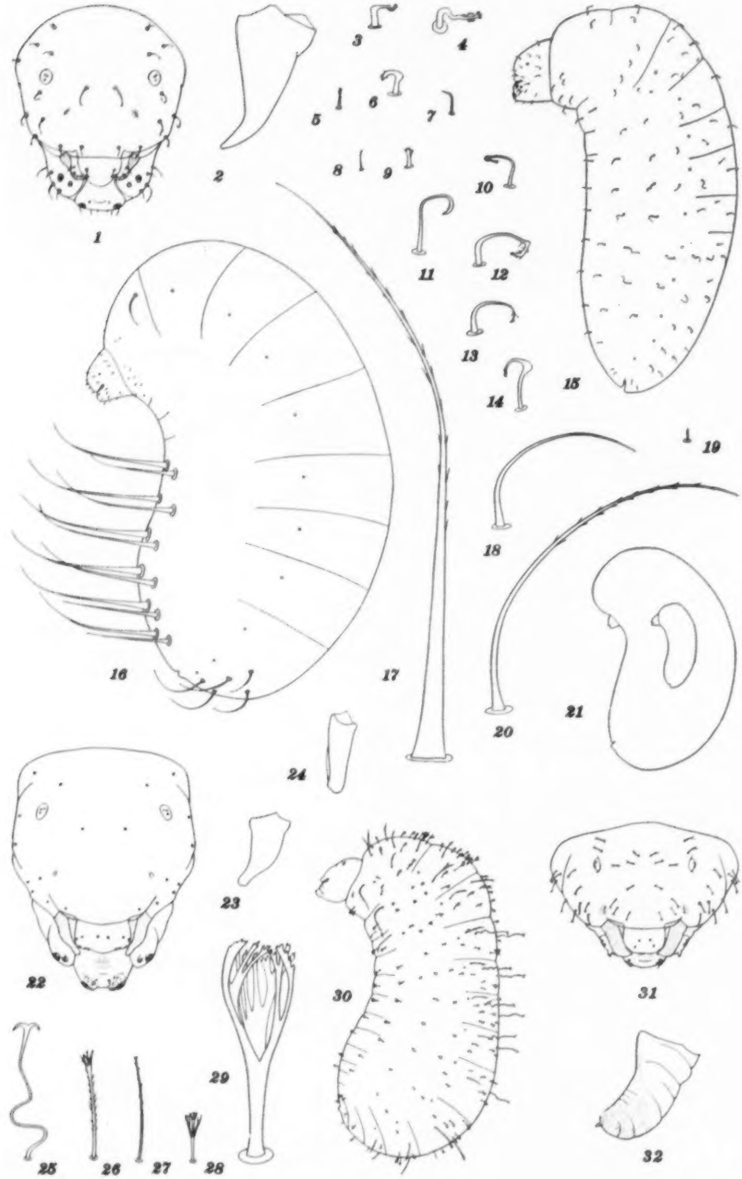
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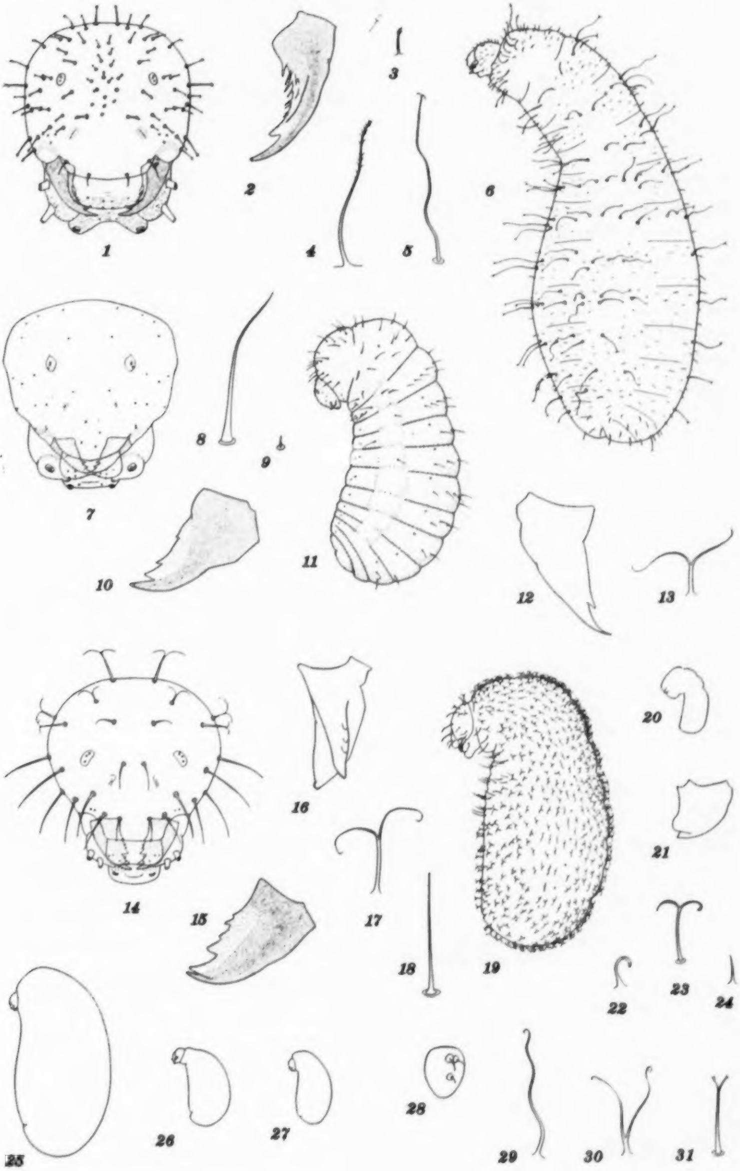
PLATE III.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Spiders of Genus Latrodectus

H. L. Keegan[1]

Dept. of Preventive Medicine, Medical Field Service School, Brooke Army Medical Center, Fort Sam Houston, Texas.

While several excellent reviews on arachnidism have been published in recent years (Bertin, 1950; Blair, 1934; Bogen, 1926; Greer, 1949; Machiavello, 1949) these have dealt primarily with the clinical problem of spider bite, and have given little information on classification of the poisonous spiders involved. Although differences in toxicity of venoms of various species of *Latrodectus* have been reported (Keegan, 1950; Shulov, 1948; Vellard, 1936) demonstrations of common antigenic properties in venoms of *L. mactans*, *L. indistinctus*, and *L. geometricus* by Finlayson and Hollow (1945) indicates need for better understanding of the relationship between members of the genus.

In this paper a brief review of the classification of spiders of genus *Latrodectus* is presented, and criteria for classification are discussed. This paper is based upon a study of the literature and upon examination of specimens from three sources. Specimens of *L. hasseltii*, *L. geometricus*, and the several described subspecies of *L. mactans* were made available by officials of the United States National Museum. Representatives of the same species, as well as *L. tredecimguttatus* and *L. menavodi* were obtained from the collections of the American Museum of Natural History through the courtesy of Dr. W. J. Gertsch. In the personal collection of the writer were specimens of *L. hasseltii*, *L. geometricus*, and *L. mactans*. Examples of *L. hystrix*, *L. pallidus*, *L. indistinctus*, *L. revivensis*, and *L. foliatus* were not available for study.

LATRODECTUS Walckenaer, 1805

Following are currently recognized species of the genus listed in the order in which they were described. Given with each valid specific name are commonly utilized synonyms which frequently appear in medical literature.

1. *L. mactans* (Fabr., 1775). Syn. *L. curacaviensis* (Muller, 1776); *L. geographicus* Van Hasselt, 1888.
2. *L. tredecimguttatus* Rossi, 1790. Syn. *L. argus* Audouin, 1826; *L. schuchii* Koch, 1836; *L. malmignatus* Walck., 1837; *L. erebus* Walck., 1837; *L. conglobatus* Koch, 1841; *L. lugubris* Motschoulski, 1849.
3. *L. geometricus* Koch, 1841. Syn. *Theridium zickzack* Karsch, 1878; *L. concinnus* Cambridge, 1905.
4. *L. menavodi* Vinson, 1863.
5. *L. hasseltii* Thorell, 1870. Syn. *L. scelio* Thorell, 1870; *L. indicus* Simon, 1897.
6. *L. katipo* Powell, 1870.
7. *L. pallidus* Cambridge, 1872

[1] Present address: U. S. Army Medical Research Unit, Institute for Medical Research, Kuala Lumpur, Malaya.

8. *L. hystrix* Simon, 1889
9. *L. indistinctus* Cambridge, 1905
10. *L. mactans texanus* Chamberlin and Ivie, 1935
11. *L. m. hesperus* Chamberlin and Ivie, 1935
12. *L. m. bishopi* Kaston, 1938
13. *L. foliatus* Mello-Laitao, 1940
14. *L. indistinctus karrooensis* Smithers, 1944
15. *L. revivensis* Shulov, 1948

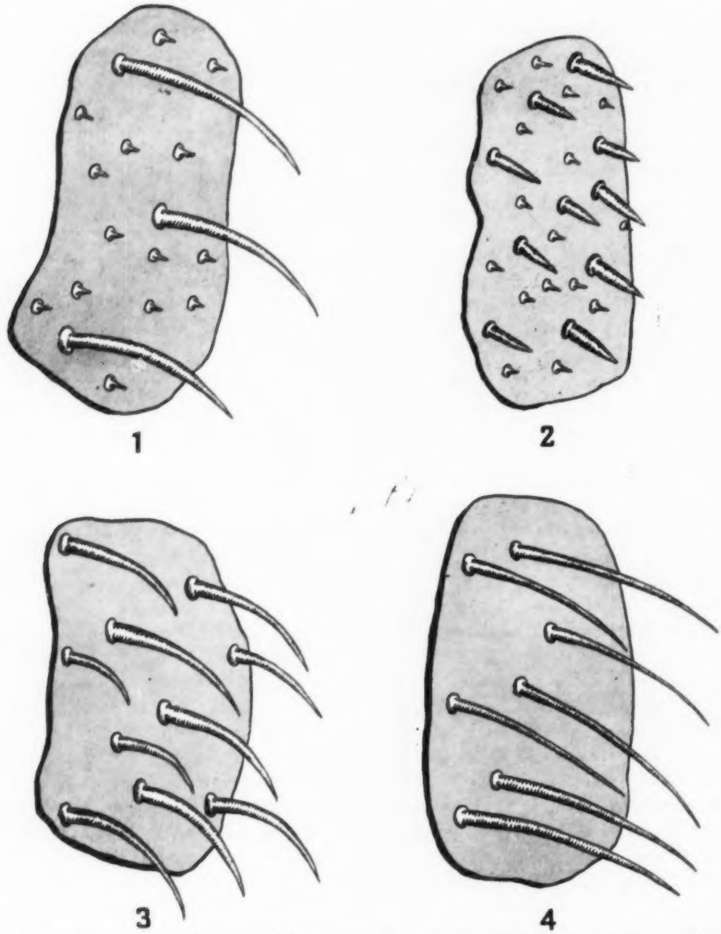
Criteria for Classification

Morphological criteria for separation of species of the genus have been difficult to select. Proposed systems of classification have been based upon variations in the following characteristics: Color pattern; arrangement of eyes, as well as their relative size; nature of setation, particularly that of the abdomen; relative length of leg pairs, and of specific leg segments; structure of the male palpi, and of the epigyne of the female; and lastly, size. Individual variations in characteristics which had been presumed to be constant led workers in various regions to describe a large number of species, most of which can now be regarded as synonyms.

This difficulty in selection of taxonomic criteria of specific value is reflected in the history of classification of spiders of genus *Latrodectus*. By 1902 a total of 43 specific names had been proposed, although Cambridge (1902a, b) who reviewed the genus at that time, recognized only five valid species. These were selected on basis of structure of the male palp, female epigyne, color pattern, relative size of eyes, and setation, and included *L. mactans*, *L. tredecimguttatus*, *L. pallidus*, and *L. hystrix*. Cambridge regarded *L. menavodi*, *L. hasseltii*, and *L. katipo* as subspecies of *tredecimguttatus*, and *L. curacaviensis* as a subspecies of *mactans*. Perhaps the most significant concept expressed in Cambridge's paper was the opinion that *tredecimguttatus*, *hasseltii*, and *mactans* were all off-shoots of one form, for which the oldest name was *mactans*. Gerschman and Schiapelli, in Sampayo's "*Latrodectus mactans* y Latrodectismo" (1942) reported that relative size of eyes was not constant, even among specimens of *geometricus*. They also found that size was not a good criterion for separation of *curacaviensis* and *mactans*, since they found many adult specimens, typically *mactans* in coloration, which were smaller than many specimens from the same areas with markings attributed to *curacaviensis*. Smithers (1944) substantiated the previous report concerning variability in eye size, and found that in a large series of *geometricus* from South Africa both eye size and arrangement of the eyes in each of the two rows were subject to considerable variation.

Comparative Aspects of Morphology

In classification of spiders, the male palp and female epigyne are structures of considerable taxonomic value. Among species of *Latrodectus* these structures are distinct in *hystrix*, *pallidus*, *geometricus*, and *revivensis* and alike in all other species. Setation and color pattern, the other characteristics most often used in separation of members of the genus, are often subject to both specific and individual variation. In this paper, the nature of such variations will be discussed and illustrated, with the aim of indicating their value as taxonomic criteria.



Figs. 1-4.—Types of dorsal abdominal setae on species of *Latrodectus*. 1. Acanthoid setae and stout, curved setae. *L. tredecimguttatus*. Corsica; 2. Short, stout, straight setae and acanthoid setae. *L. hystrix*. Yemen. Redrawn from Cambridge (1902); 3. Stout, curved setae. *L. hasseltii*. Luzon; 4. Slender, slightly curved setae. *L. geometricus*. Luzon.

SETATION OF THE DORSAL SURFACE OF THE ABDOMEN AS A TAXONOMIC CRITERION

There are four types of dorsal abdominal setae on species of *Latrodectus*. These are:

Acanthoid setae (fig. 1).[2]—Found on *pallidus, hystrix, revivensis, tredecimguttatus,* and *hasseltii*. Presence of this type of short, thorn-like seta is apparently a constant

[2] All figures are of adult female specimens. Geographic point of origin of specimen is cited with each figure.

characteristic of all these species but *hasseltii*. The writer has examined specimens of *hasseltii* from New Guinea, Luzon, and Tinian which lack acanthoid setae, and Cambridge (1902) figures specimens from India and the Loyalty Islands which do not possess them.

Short, stout, straight setae (fig. 2).—Found on *hystrix, revivensis,* and *indistinctus*. Although Smithers (1944) lists presence of such setae as a characteristic of *indistinctus*, the writer has examined two Madagascar specimens with markings typical of *indistinctus*, which do not possess setae of this type.

Stout, curved setae (fig. 3).—Found on *tredecimguttatus, hasseltii,* and *indistinctus*. These are said to be always present on *tredecimguttatus*. They are present on two adult female specimens of *hasseltii* from Luzon, but lacking on specimens of the same species from New Guinea and Tinian Island. Cambridge's specimens from India and the Loyalty Islands did not possess them.

Slender, slightly curved setae (fig. 4).—Found on *mactans* and its subspecies, also on *geometricus, menavodi* and *katipo*, as well as some specimens of *hasseltii*.

COLOR PATTERN AS A TAXONOMIC CRITERION

When the extent of individual variation is recognized, differences in color pattern are excellent criteria for separation of species of the genus. In considering relationships of the darker species, both adult and juvenile color patterns should be examined. As in other spiders, dorsal and lateral markings on the abdomen often coincide with points of muscle attachment. Each of the lighter colored species (*pallidus, geometricus, revivensis,* and *hystrix*) has a distinct color pattern, which, in spite of individual variation, shows no interspecific overlapping. This is not always the situation among the darker species (*mactans, bishopi, indistinctus, hasseltii, katipo, menavodi, tredecimguttatus,* and *karrooensis*) where four basic color patterns occur, and individuals of different species, and from widely separated areas, may be nearly identical in appearance. In such cases it will be found however, that the populations as a whole show distinct differences, and that juvenile specimens possess distinctive markings, even when individual adults are alike in coloration. Basic color patterns of the dark species of the genus are:

Abdomen entirely black or brown dorsally. The ventral hour-glass markings may be incomplete or lacking in some adults. Examples of this melanistic type of coloration may be found in individuals of *mactans, tredecimguttatus,* and perhaps in *menavodi*.

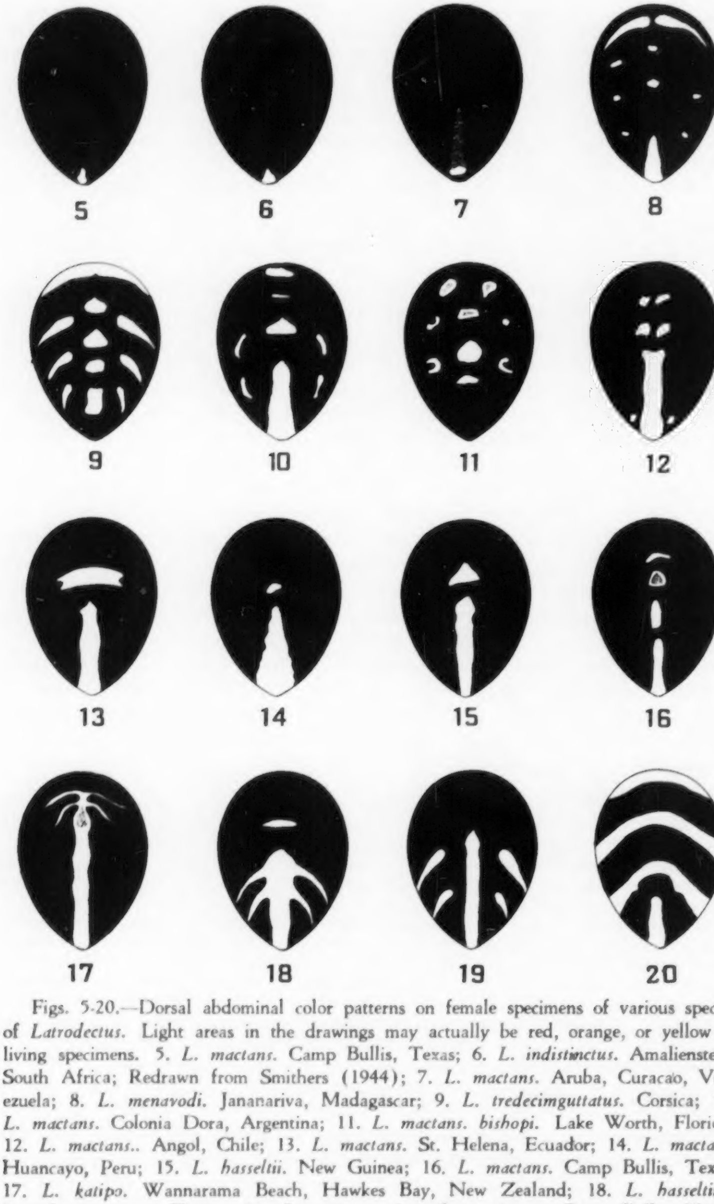
Abdomen dorsally with a red, yellow, or orange marking above the spinnerets and ordinarily with no other dorsal markings except small, irregularly arranged dots. Such an appearance is found in examples of *indistinctus* and *mactans* (figs. 5-7).

Abdomen with a posterior dorsal marking as in 2, and with additional mid-dorsal and lateral markings, producing a spotted appearance. This type of pattern is seen in specimens of *tredecimguttatus, menavodi, bishopi, indistinctus,* and *texanus* (figs. 8-11).

Abdomen with a mid-dorsal stripe, which may be solid or broken into a series of spots anteriorly. Lateral markings are usually elongated streaks, rather than rounded or rectangular in shape. Such markings are found on specimens of *hasseltii, mactans,* and *karrooensis* (figs. 12-17). In *mactans* the lateral markings are rarely confluent with the mid-dorsal stripe, while the opposite is true of *hasseltii* and *karrooensis*.

COMPARATIVE FEATURES IN BIOLOGY OF SPECIES OF LATRODECTUS

Studies in comparative biology of species of the genus have been few in number, perhaps due to the fact that most of the species are geographically isolated. Field observations and laboratory experiments sufficiently detailed to be of value have dealt with comparative toxicity of venom, common antigenic factors in venom, web structure, and egg sack production.



Figs. 5-20.—Dorsal abdominal color patterns on female specimens of various species of *Latrodectus*. Light areas in the drawings may actually be red, orange, or yellow in living specimens. 5. *L. mactans*. Camp Bullis, Texas; 6. *L. indistinctus*. Amalienstein, South Africa; Redrawn from Smithers (1944); 7. *L. mactans*. Aruba, Curacao, Venezuela; 8. *L. menavodi*. Jananariva, Madagascar; 9. *L. tredecimguttatus*. Corsica; 10. *L. mactans*. Colonia Dora, Argentina; 11. *L. mactans. bishopi*. Lake Worth, Florida; 12. *L. mactans*.. Angol, Chile; 13. *L. mactans*. St. Helena, Ecuador; 14. *L. mactans*. Huancayo, Peru; 15. *L. hasseltii*. New Guinea; 16. *L. mactans*. Camp Bullis, Texas; 17. *L. katipo*. Wannarama Beach, Hawkes Bay, New Zealand; 18. *L. hasseltii*—juvenile specimen. Tinian; 19. *L. mactans*—juvenile specimen. Camp Bullis, Texas; 20. *L. indistinctus*—juvenile specimen. Humansdorp, Cape Prov., South Africa.

In this discussion an attempt is made to review published observations on these aspects of biology.

Comparative toxicity of venom.—Shulov (1948), using *Microtus guentheri* as an experimental animal, found that the venom of *revivensis* was similar in toxicity to that of *tredecimguttatus,* and more toxic than that of *pallidus.* Finlayson (1945) found *indistinctus* venom more potent than *geometricus* venom for rabbits as evidenced by respective MLDs of 3mg and 12mg. Keegan, Blauw, and Anderson (1950) found that *geometricus* venom was less toxic for mice and guinea pigs than venoms of *mactans* and *hasseltii.* D'Amour et al (1936) found that toxicity of *mactans* venom may vary with age of specimen, locality and season.

Common antigenic properties of venom.—Finlayson (1945) demonstrated that antivenine produced by inoculation of goats with *indistinctus* venom was also effective in treatment of bites of *geometricus,* but that the reverse was not complete. Sampayo (1942) and Finlayson (1945) found that anti-mactans serum produced in South America neutralized *indistinctus* venom at high dilutions. The reverse was not attempted.

Web structure.—Although several workers (Cambridge, 1902; Hornabrook, 1951; Kaston, 1938; Pearson, 1936; Smithers, 1944) have reported slight specific differences in web structure and location, the only conspicuous differences are displayed by *karrooensis* and *bishopi,* both of which construct webs off the ground in bushes. *L. karrooensis,* which occurs in South Africa along with *indistinctus,* is unique in that it adds small rocks to its web (1944), and *bishopi,* alone among the species of *Latrodectus,* builds a sheet-like web. The latter species builds webs in palmettoes, and is often associated with the nest of a small wasp (1938). The writer has seen a series of *mactans* collected from occupied nests of the harvester ant *Pogonomyrmax barbatus.* These specimens were collected at Camp Bullis, Texas in November 1951.

Egg sack production.—Varies with availability of food, temperature, and perhaps other environmental factors. Smithers (1944) reported that spiders fed very little produced small egg-sacks and fewer egg sacks. *L. geometricus* is distinct in producing egg-sacks studded with silken tubercles. Rate of development of eggs varies with temperature (Shulov, 1948; Smithers, 1944). Smithers found that numbers of egg sacks produced differed among specimens observed in the field and those kept in the laboratory. Keegan et al (1950) and Smithers (1944) obtained slightly different figures for egg sack production of *geometricus* in the Philippines and in South Africa respectively. Shulov (1948) found the incubation period for *revivensis* eggs less than for eggs of *pallidus* and *tredecimguttatus* taken in Palestine under similar conditions of temperature and humidity. The work of Lawson (1933) as well as D'Amour et al (1936) has revealed the variability of egg sack production by *mactans.*

DISTINGUISHING CHARACTERISTICS AND GEOGRAPHIC DISTRIBUTION OF SPIDERS OF GENUS LATRODECTUS

LATRODECTUS MACTANS (Fabr., 1775)

Distinguishing characteristics.—Dorsal surface of abdomen entirely black, or with markings of red, yellow, or white which range in extent from a small red spot above the spinnerets to a mid-dorsal line, or series of mid-dorsal spots with lateral markings as well. When lateral markings are present, they are rarely connected with the mid-dorsal line, except at the posterior end of the body immediately dorsal to the spinnerets. There is considerable individual variation in color pattern, and specimens from Mexico, Central, and South America show the greatest amount of red or yellow on the dorsum. The ventral hour-glass is often typical in shape, but may be incomplete or absent. Setae of abdomen are relatively long and slender, and may vary in length, but not in type. All color varieties are alike in structure of epigyne and male palp.

Distribution.—North, Central, and South America, adjacent coastal islands, the West Indies, and the Hawaiian Islands. Records from the United States and Canada are reviewed by Becker et al (1936). A general review of the distribution is presented by Vellard (1936), and distribution in South America is discussed by Gerschmann and Schiapelli in Sampayo (1942). Occurrence of the species in Central America was reported by Pickard-Cambridge (1905). Mexican specimens in the collections of the United States National Museum include spiders from states of Oaxaca; Guerrero; and Jalisco.

SUBSPECIFIC NAMES

Chamberlin and Ivie (1935) revised the classification of North American *mactans* and described two subspecies based, for the most part, upon differences in color pattern.

LATRODECTUS MACTANS MACTANS (Fabr., 1775)

Distinguishing characteristics.—Abdomen shiny black with a red spot above spinnerets, or with red spots, which may extend along the dorsum for much of its length as a median band, or may be broken into a number of spots. Hour-glass marking present, but not always typical in shape. Red mark above spinnerets is ordinarily only mark on dorsum, and is more or less oval in shape.

Distribution.—Eastern United States from New Hampshire to Florida and westward to Texas and Oklahoma. Probably extends down gulf coast into Mexico. *Type locality:* Massachusetts.

LATRODECTUS MACTANS TEXANUS Chamberlin and Ivie, 1935

Distinguishing characteristics.—Differs from *m. mactans* in being larger on average, and possessing longer legs. Dorsum of abdomen most often black with a red streak above spinnerets, usually accompanied by a small, white mark at anterior end, and sometimes by lateral markings. In a series of adult female specimens taken at Camp Bullis, Texas there is marked individual variation in color pattern. Males are said to be much lighter in color than in *m. mactans.*

Distribution.—Most of Texas, extending into other southwestern states, into California, and northward into southern Utah. Undoubtedly extends into Mexico. Is the most common form in Texas, but is rare westward from there. *Type locality:* Alvarado, Texas.

LATRODECTUS MACTANS HESPERUS Chamberlin and Ivie, 1935

Distinguishing characteristics.—Never a red mark on dorsum. Red spot on venter typically hour-glass shaped, but may vary, or be absent. The male is said to vary greatly in size and solor.

Distribution.—Abundant in all states west of the Rocky Mountains; into Canada on the north. Lower California and northern Mexico on the south. In the southern U. S. extends eastward into western Texas. Type locality: Salt Lake City, Utah.

Discussion.—It will be noted that the subspecific categories of Chamberlin and Ivie do not adequately describe specimens of *mactans* from Mexico, as well as Central and South America. A form of *mactans* found in several South American countries was described as a separate species, *L. curacaviensis* (Muller, 1776) because of its small size. However, Gerschmann and Schiapelli considered this criterion to be of doubtful value, since they found specimens, typically *mactans* in coloration, which were smaller than other specimens from the same localities, which had been identified as *curacaviensis.* Examples of variation in color pattern are shown in figs. 21-25.

LATRODECTUS MACTANS BISHOPI Kaston, 1938

Distinguishing characteristics.—This subspecies is distinctive in that the cephalothorax and legs are bright orange in color in most specimens, but may be yellow or brick red. Markings on the dorsal surface of the abdomen are arranged much as in *tredecimguttatus* (fig. 26). None of sixty one specimens examined by Kaston had a complete, ventral, hour-glass marking. Webs of this subspecies are constructed from three to four feet or more off the ground, and are often associated with the nest of a wasp near the bases of palmetto leaves. The web is sheet-like in structure instead of the typical irregular, network common among spiders of family *Theridiidae.*

Distribution.—Has been found only at Lake Worth, Florida. Kaston (1938).

LATRODECTUS TREDECIMGUTTATUS Rossi, 1790

Distinguishing characteristics.—Dorsal surface of abdomen typically black or brown with a series of red, yellow, or whitish spots (fig. 9), but may be entirely black. In the only female specimen available for study the hour-glass marking on the ventral surface of the abdomen is incomplete. There are two types of dorsal abdominal setae: one

long, stout and curved, the other acanthoid (fig. 1). The latter are more numerous.

Distribution.—The Mediterranean region including portions of southern Europe, Asia Minor, Arabia, and northern Africa. It has also been collected at Bushire, on the Persian Gulf. In Europe the species has been reported from Greece, France, Italy, Sardinia, Corsica, Spain, Russia, and Yugoslavia. It has also been taken from the Canary and Madeira Islands. In Asia Minor it is found in Palestine, and in northern Africa occurs in Egypt, the Sudan, the French Morocco. General distribution of this species was reviewed by Cambridge (1902), and Vellard (1936). Recent records from Yugoslavia are given by Maretic (1951); from Russia by Marikovskii (1948); from Palestine by Shulov (1948); and from Morocco by Gaud and Delaselle (1949).

LATRODECTUS GEOMETRICUS Koch, 1841

Distinguishing characteristics.—Eyes of anterior median pair usually larger than the remainder. Ground color of abdomen varies from pale yellow to almost black; with median and lateral dorsal marking. Ventral hour-glass marking always present. Abdomen with relatively long, slender setae. These may be of varying length, but are all of same type. In addition to the distinctive epigyne and male palpal structure, this species is distinct in that egg sacks are provided with silken tubercles.

Distribution.—The most cosmopolitan species of the genus. Has been reported from both Old and New World localities; specifically from North, South, and Central America, adjacent coastal islands, Hawaiian Islands, the Philippines, Africa, India and Australia. Distribution of this species is reviewed by Cambridge (1902), Keegan et al (1950), Pearson (1936) and Smithers (1944).

LATRODECTUS HYSTRIX Simon, 1889

Distinguishing characteristics.—No specimens of this spider were available for study. According to Cambridge (1902a, b) the species is distinctive in possessing two types of abdominal setae; acanthoid spines, and short, stout, relatively straight setae. The color variation is not known, but as illustrated by Cambridge, the color is dark with three lighter cross-bands which include a number of small, whitish spots. In the specimen figured there is a longitudinal series of three pairs of small, dark spots on the dorsal surface of the abdomen at the points of muscle attachment.

Distribution.—Reported from Arabia, specifically from Yemen and Aden, by Cambridge (1902).

LATRODECTUS PALLIDUS Cambridge, 1872

Distinguishing characteristics.—No specimens of this species were available for study. Descriptions by Cambridge (1902) and Shulov (1948) indicate that the species is distinctive in that the abdominal integument is almost smooth, except for minute, acanthoid spines laterally. The dorsal surface of the abdomen is creamy yellow-white with a series of four deep red-brown spots forming an oblong about the center of the dorsal surface. There are several additional very small, dark spots beside and behind the larger ones.

Distribution.—Reported from Palestine, and from Bushire, on the Persian Gulf, by Cambridge (1902); more recently from Palestine by Shulov (1948).

LATRODECTUS KATIPO Powell, 1870

Distinguishing characteristics.—Differs from *hasseltii* in that legs of the first pair are relatively shorter, and theoretically in absence of acanthoid setae. Since the presence of acanthoid setae is not constant even in *hasseltii,* and the extent of variation in leg length is not accurately known, the subspecific status of *katipo* is at least open to question. In the one female specimen examined by the writer, the ventral hour-glass marking was not complete (fig. 17).

Distribution.—New Zealand. Powell (1870), Cambridge (1902), Taylor and Murray (1946), and Hornabrook (1951).

LATRODECTUS HASSELTII Thorell, 1870

Distinguishing characteristics.—Dorsal surface of the abdomen with a median, red or yellow longitudinal band. This may be constricted anteriorly, and in some specimens there may be one or more spots anterior to the band proper. In all juvenile, and some adult specimens there are lateral markings extending from the median band. Whenever

lateral markings are present they are connected with the central band. In this respect *hasseltii* differs from *mactans*, but not from *indistinctus*. The ventral hour-glass may or may not be present. Although Cambridge (1902a, b) states that the species possesses acanthoid setae, as well as longer setae, the former were not present on specimens examined by the writer and which had been taken on New Guinea, Tinian Island, and from Luzon Island in the Philippines. The two female specimens from Luzon possessed only long, stout, curved setae, while the other specimens possessed only long, slender setae very much like those of *mactans* and *geometricus* (figs. 30-35).

Distribution.—India, Australia, New Caledonia, the Loyalty Islands, Timor, Morotoi, the Maldive Islands, New Guinea, the Philippines, and the Marianas. Early records from Africa, Burma, and India have not been substantiated in recent years. Cambridge (1902) reviewed the distribution of the species, while more recent records are given by Plantilla and Mabalay (1932), Sloggett (1946), Taylor and Murray (1946) and Keegan et al (1950).

LATRODECTUS MENAVODI Vinson, 1863

Distinguishing characteristics.—Differs from *tredecimguttatus* in that the dorsal spots are reduced to small dots, and that acanthoid setae are lacking. It also differs from *indistinctus* in the latter respect, but some adult female specimens may be indistinguishable from specimens of *mactans* from the United States. In six female specimens from Jananariva, Madagascar there was considerable variation in dorsal color pattern, as well as in the ventral hour-glass markings (figs. 27-29). Four of these specimens possessed long, slender, dorsal abdominal setae, while in the remaining two the abdominal setae were relatively shorter, stout and curved.

Distribution.—Madagascar. Cambridge (1902), Vellard (1936).

LATRODECTUS INDISTINCTUS Cambridge, 1905

Distinguishing characteristics.—No specimens of this species were available for study. Dorsal surface of abdomen jet black, or with a series of small, white dots. A red spot, or subtriangular patch dorsal to the spinnerets. In adult specimens the hour-glass marking on the venter is incomplete, and in some specimens may be absent. Dorsal surface of abdomen with setae of three types: long, stout, curved; medium curved; and short, straight (acanthoid) in ratio of 8:3:2. While the color pattern of adult *indistinctus* may be exactly duplicated by specimens of *mactans*, the manner in which the color pattern is developed is quite different. This may be seen by comparing Smither's figures of developmental stages of *indistinctus* with color patterns of juvenile *mactans* from Texas (figs. 6, 19, 20, 34).

Distribution.—South Africa. Smithers (1939, 1944).

LATRODECTUS INDISTINCTUS KARROOENSIS Smithers, 1944

Distinguishing characteristics.—Dorsal surface of abdomen jet black with a distinct red, median, longitudinal band, the anterior end of which is produced into two arms laterally, forming a T-shaped marking. This subspecies occurs with *indistinctus* in the Karroo region of South Africa, and according to its describer, constructs its web off the ground in low bushes. It is also distinct in weaving small pebbles into its web. Smithers reports that some of these are almost as large as the abdomen of the spider (fig. 35).

Distribution.—Has been found only on the Karroo Plateau of South Africa. Smithers (1944).

LATRODECTUS FOLIATUS Mello Laitao, 1940

Distinguishing characteristics.—No specimens of this spider were available for study. Gerschmann and Schiapelli (1942) noted that the species was very close to *geometricus*, from which it varied in that the male palpal structure was like that of *mactans*. Color pattern, as figured, differs from that of *geometricus*, and the anterior median eyes are not larger than the others.

Distribution.—Reported only from the Province of Buenos Aires, Argentina. Mello Laitao (1940), Gerschmann and Schiapelli in Sampayo (1943).

LATRODECTUS REVIVENSIS Shulov, 1948

Distinguishing characteristics.—No specimens were available for study. The following details are from Shulov's original description. Abdomen varies from black with a

Figs. 21-35.—Dorsal abdominal color patterns on female specimens of various species of *Latrodectus*. 21. *L. mactans*. Camp Bullis, Texas; 22. *L. mactans*. St. Helena, Ecuador; 23. *L. mactans*. Huancayo, Peru; 24. *L. mactans*. Ninabamba, Rio Pampa, Peru; 25. *L. mactans*. Colonia Dora, Argentina; 26. *L. mactans bishopi*. Lake Worth, Florida; 27. *L. menavodi*. Jananariva, Madagascar; 28. *L. menavodi*. Jananariva, Madagascar; 29. *L. menavodi*. Jananariva, Madagascar; 30. *L. hasseltii*. Luzon; 31. *L. hasseltii*. Tinian; 32. *L. hasseltii*. New Britain. Redrawn from Cambridge (1902); 33. *L. hasseltii*. Karachi. Redrawn from Cambridge (1902); 34. *L. indistinctus*. Manire, Malmesburg Div. South Africa. Redrawn from Smithers (1944); 35. *L. indistinctus karrooensis*. Laingsburg, Cape Prov., South Africa. Redrawn from Smithers (1944).

brownish hue to yellowish gray, with only four less distinct central points, sometimes with grayish marking around them. Hour-glass marking incomplete in adults. Dorsal surface of abdomen with dense, short, straight setae. Color of cephalothorax varies from almost black to dull brown with white pubescence. Legs in dark specimens are almost black.

Distribution.—Southern Palestine. Shulov (1948).

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The Gnathosoma of the Celaenopsina, (Acarina—Mesostigmata)*

Flora E. Gorirossi
North Carolina State College, Raleigh

In the present paper the gnathosomal structures of *Euzercon latus* (Banks), 1909 and *Passalacarus sylvestris* Pearse and Wharton, 1936, representatives of the families Euzerconidae and Diplogyniidae, respectively, are described and figured. The two species are found on passalid beetles and were collected from the Duke University Forest, Durham, N. C. The methods discussed in the paper on *Megisthanus floridanus* (Gorirossi and Wharton, in press) were used for the present study.

Oudemans in 1928 described, among others, the gnathosomal structures of *Euzercon ovale* Kramer, 1927, a member of the family Euzerconidae and the gnathosomal structures of two species which belong to the Diplogyniidae: *Diplogynium indica* (Oudemans), 1927 and *Diplogynium tropica* (Oudemans), 1927. Plate II contains for comparison with the gnathosomal elements of *E. latus* and *P. sylvestris* figures of dissections of the gnathosoma of these three species which are taken after Oudemans. In the legend for the symbols used, Oudemans original description is included in parentheses next to the terminology now employed.

The author wishes to express her gratitude to Dr. G. W. Wharton of Duke University for his help during the course of this study.

Habits.—Pearse et al. (1936) conducted an extensive survey on the ecology of the passalid beetle and the parasites associated with it. They discovered that adults of both *E. latus* and *P. sylvestris* are found on the beetle throughout the year except for the months of June, July and August. Trägårdh (1950) in discussing the ecology of the Diplogyniidae concluded that since the adult forms are the only forms found on the passalid, that they and not the immature stages emigrate to new breeding quarters. He inferred that the mites undergo their development in the same biotope as the beetles, i.e. in rotting logs and tree stumps. As suggested by Trägårdh "an investigation of the fauna of the rotton logs where the larvae of the beetles live would undoubtedly be rewarded by the discovery of the postembryonal development of the Diplogyniidae which would be a most welcome addition to our as yet rather meagre knowledge of this family."

Euzercon latus (Banks), 1909

Gnathosoma.—The gnathosoma of *E. latus* projects from the anteroventral surface of the ellipticaly-shaped idiosoma. It is round in shape and heavily sclerotized. The posteroventral margin of the gnathosomal ring is between coxae I and II. The gnathosoma of the males and females exhibit sexual dimorphism. That of the female is typical, i.e. it exhibits all the features

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normally associated with the gnathosoma of the mesostigmatid mites. In the male, however, the hypostomal region of the gnathosoma is modified. The hypostomal walls, processes and setae are replaced with anteriorly projecting structures probably associated with sperm transfer. A striking feature of the gnathosoma of both sexes is the dorsal row of hypopharyngeal teeth which are readily seen from the ventral view.

Gnathosomal base.—(Pl. I A, C) The medioventral surface of the gnathosomal base of the male (C) is delineated by synarthrodial membranes from its lateral and dorsal surfaces as well as the hypostomal and protosternal regions. The membranes extend in an oblique line from the posterolateral sides of the gnathosomal base to the region around the base of the protosternum. Included between the membranes are the deutosternum, the gnathosomal setae and a small portion of the gnathosomal base which borders the lateral and posterior surfaces of the deutosternum. On the lateral sides of this restricted portion of the base, between the gnathosomal setae and its posterolateral margins are ten to fifteen, tiny, anteriorly projecting teeth arranged in a semicircle. Additional ornamentation occurs on the lateral sides of the gnathosomal base, just posterior to the palpal trochanter and lateral to the tectum. There are four rows of teeth similar to the teeth on the ventral portion of the base. They are more or less evenly spaced; the most distal row is on the anterior margin of the base and the most posterior row is a little anterior to the posterior margin of the tectum. The numbers of teeth per row varies from approximately fifteen in the most anterior row to approximately thirty-five in the most posterior row.

The gnathosomal base of the female (A) conforms to the typical structure found in the Mesostigmata. Unlike that of the male, it lacks the delineating membranes, and its ventrolateral walls are continuous with those of the hypostomal walls. The ornamentation present in the male is present in the female. The only difference is that the teeth are not as strongly developed as they are in the male.

Deutosternum.—The deutosternum (u) of the female measures 184 microns from tip to base. It has five lines of teeth which appear to be the emarginate surfaces of five contiguous, lightly sclerotized plates. The plates are arranged one behind the other all subequal in length and width. The teeth on the posterior three plates are more conspicuous than on the anterior two.

The deutosternum of the male is similar to that of the female. It is shorter (61 microns) and possesses two, lightly sclerotized plates with serrated edges. The two plates, however, appear to be formed by two lateral plates which have insensibly fused along their medial surfaces.

Gnathosomal setae.—The gnathosomal setae (w) of the male are long (98 microns), slender structures which possess scattered, delicate setules over their surfaces. They are anterior to the most anterior row of deutosternal teeth, and are at the anterior apices of the restricted portion of the gnathosomal base. The gnathosomal setae of the female are more slender than those of the male and measure 61 microns. They are shorter than any of the hypostomal setae and are covered with strong setules along the anterior two-thirds of their length. They arise at the level of the third row of deutosternal teeth.

Horizontal shelf.—(Pl. II C) The horizontal shelf of *E. latus,* comprised of the subcheliceral plate, the epistome and the tentorium, is heavily sclerotized. It is quite similar to that found in *M. floridanus.*

Subcheliceral plate.—The bars of the subcheliceral plate (d) measure 181 microns long. They project to the metapodosomal region of the idiosoma. They are relatively narrow and when viewed from the ventral or dorsal surface appear to arch outward about midway along their length. The bridge which connects them posteriorly and from which the epipharyngeal muscles originate is heavily sclerotized.

Epistome.—The epistome (i) supports the labrum as it does in *M. floridanus.* It is not, however, as heavily sclerotized as is the epistome of *M. floridanus.*

Tentorium.—The tentorial region (m) is restricted to the epistomal region of the horizontal plate.

Cheliceral sheaths.—(Pl. III A, B) The inner and outer cheliceral sheaths (a′, a″), their insertion and origin are similar to those of *M. floridanus.*

Pharynx.—(Pl. III A) The pharynx (s) of *E. latus,* like that of *U. agitans* (Gorirossi, in press) is triangular in shape. It, too, possesses lateral dilator muscles which originate from the ventrolateral walls of the gnathosomal base and insert on its ventrolateral walls, dorsolateral dilator muscles which originate from the ventrolateral surfaces of the epistome and insert on the lateral regions of its dorsal wall, and constrictor muscles which insert on its corners and alternate with the dilator muscles.

Tectum.—(Pl. I E, F) The tecta of the male and female are essentially the same and will be included in the following description. The tectum of the male measures 246 microns from tip to base and 246 microns at its widest portion; that of the female measures 246 microns from tip to base and 255 microns at its widest portion. The sculpturing of the tectum readily differentiates it from the adjoining walls of the gnathosomal base. The posterior half of the tectum is rectangular in shape, and wider than it is long; more anteriorly, the sides converge and the tectum becomes triangular in shape. The posterior region is fused to the lateral and posterior walls of the gnathosomal base, but its anterior portion projects beyond the mouth parts. On the dorsal surface of the tectum are numerous rows (twelve on one female specimen examined) of tiny, wedge-shaped teeth which point anteriorly. Many occur in parallel series, others have no consistent pattern and still others extend to the sides of the tectum. The majority, however, are concentrated in the central posterior two-thirds of the tectum. Anterior to these rows of teeth are tiny lines which lack teeth and run more or less parallel with the sides of the tectum. From each edge of the triangular portion of the tectum is a lightly sclerotized extension which gradually widens posteriorly. Just anterior to its posterior termination, the extension dips to the edge of the tectum. It contains no ornamentation. From the medial, ventral surface of the tectum in its posterior half, is a thin, slightly sclerotized keel which projects into the idiosoma. It serves for the attachment of the inner and outer cheliceral sheaths. Anterior to this keel and separated from it is a slender, conical tooth which is elliptical in cross section. It is 55 microns long in the female and 77 microns long in the male.

It projects freely from its attachment and probably serves to separate the chelicerae.

Epipharynx.—(Pl. II B; Pl. III B-I) The epipharynx (j) is 194 microns long. In cross section it is diamond-shaped. Compared with the epipharynx of *M. floridanus* and *U. agitans*, the epipharynx of *E. latus* is simply ornamented. Its ventrolateral sides are heavily sclerotized and have no ornamentation. Its dorsolateral sides are lightly sclerotized and appear almost membranous. They are densely covered with small spines.

Epipharyngeal styli.—Pl. II C, D) The epipharyngeal styli (f) are needle-like structures which are found dorsal to the epipharynx and lateral to the labrum. Their sides are serrated. They are approximately 27 microns long and are found in both sexes.

Labrum.—(Pl. II B, C; Pl. III C-E) The labrum (h) is 49 microns long and projects from the epistome. It is a hollow structure and shaped like a spatula. Its walls are lightly sclerotized and densely covered with small spines.

Hypopharynx.—(Pl. II A; Pl. III B-I) The walls of the hypopharynx (q) originate at the posterior limit of the hypostome and extend the length of the protosternum. Its lateral walls are reinforced by heavily sclerotized apodemes which are continuous ventrally with the lateral walls of the protosternum. Only in the proximal region of the hypostome are hypopharyngeal, dilator muscles (x) present. These originate from the ventrolateral walls of the hypostome and insert on the ventrolateral walls of the hypopharynx. The walls of the hypopharynx are lightly sclerotized and densely covered with tiny spines.

Hypopharyngeal styli.—(Pl. II A, C-E; Pl. III B-E) The hypopharyngeal styli (v) occupy the same position as those in *M. floridanus* and *U. agitans*. They are relatively short structures (61 microns long) and not as slender as those found in *M. floridanus* or *P. sylvestris*. They are hollow, lightly sclerotized, and covered with small spines.

Hypostome.—(Pl. I A, C; Pl. III B-H) The hypostomal region (k) in the female (A) projects freely on either side of the protosternum. The walls are continuous posteriorly with the ventral walls of the gnathosomal base. More anteriorly their medial surfaces curve outwardly and the walls of the hypostome become considerably narrower.

Hypostomal setae.—(Pl. I A, C) The hypostomal setae are arranged in a pattern similar to those of *M. floridanus*. They are restricted to the narrow, anterior portion of the hypostome. Each occupies the corners of a triangle, the longest side of which connects the distal and the medial setae. The medial and the lateral setae each possess tiny setules, the distal setae are nude. The distal seta (92 microns long) is the shortest of the hypostomal setae, but is the most robust. The medial seta (147 microns long) is the longest of the hypostomal setae and similar in appearance to the lateral seta (107 microns long).

As mentioned previously, the hypostomal region (k″) of the male (C) is modified and possesses structures which possibly aid in sperm transfer. The modifications are restricted to the anterior portion of the hypostomal region;

the posterior portion is the same as described for the female. The sides of the hypostome are asymmetrical. The right side contains two processes. One, the taller and more lateral in position of the two, measures 92 microns long. It is heavily sclerotized and immovable. The other process is 30 microns tall and about as wide as it is tall. It appears to be joined to the posterior wall of the hypostome by a membrane and therefore might be movable. It is heavily sclerotized, shaped like a knob and in fixed preparations always lies over the ventral surface of the protosternum. The left side of the hypostomal region is quite different from the right side. It has three different structures. The tallest of these (215 microns) is immediately lateral to the protosternum and rises well above the tip of it. It is a slender, heavily sclerotized, rod-like structure which appears to be movable. The distal, medioventral portion of it is densely covered with short spines. Extending along its lateral surface and projecting slightly beyond it anteriorly is a lightly sclerotized excrescence. It is smooth in texture and swirles around the base of the more heavily sclerotized, rod-like portion. The two remaining structures are more lateral in position and immovable. The more lateral of the two is the taller (27 microns). It resembles a slender tooth. The other structure is the smallest of all the hypostomal processes. It is so oriented that its lateral side is perpendicular to the long axis of the body of the mite and lies just posterior to the two former processes described. It terminates in a rounded protuberance.

Protosternum.—(Pl. I A, C; Pl. II D, E; Pl. III B-I) The protosternum (y), which in *M. floridanus* and *U. agitans* is flanked on either side by the hypostomal walls, in *E. latus* projects freely between the hypostomal region. It forms a shallow trough (138 microns long in the male; 123 microns long in the female) which protects the floor of the hypopharynx. Cross sections of the protosternal region of *E. latus* show a pair of heavily sclerotized apodemes (r) which originate on either side of the walls of the hypopharynx and lend support to it. These fuse with the lateral walls of the protosternum. They are covered laterally by lightly sclerotized membranes (r′) which originate from the dorsal wall of the hypostome (k′) and insert on the dorsal edge of the apodeme at a junction with the walls of the hypopharynx (q′). The dorsal edge of this lateral, membranous covering of the apodeme is dentate. The degree of dentation varies in size from short, anteriorly, to long, medially, to short again, posteriorly. Since this apodeme is associated with the hypopharynx, the teeth of the membrane which extend along the dorsal edge of the hypopharynx are referred to as the most dorsal row of hypopharyngeal teeth (g). These teeth are very conspicuous from a ventral view of the gnathosoma and radiate from either side of the protosternal region like the sticks of a fan. There are approximately 50 teeth on each side. The anlage of the apodeme, i.e. whether it is of hypostomal or protosternal origin or of some other origin cannot be determined from the present study.

Hypopharyngeal processes.—(Pl. I A, C; Pl. II A, C) These processes (o) extend distally beyond the apodemes as separate processes. Each process is forked.

Hypostomal processes.—(Pl. I A, C; Pl. II C) These processes (p) are lacking in the male. In the female they are lightly sclerotized, blade-like structures which project freely between the protosternal and the hypostomal regions.

Their medial surfaces are continuous with the medial surfaces of the walls of the hypostome and their lateral surfaces connect with the medial surfaces of the hypostome between the distal and the lateral hypostomal setae. The sides of the processes in some specimens are deeply serrated, in others they are slightly serrated, and still in others they are smooth. They are 107 microns long.

Corniculi.—Pl. I A, C; Pl. II C) The corniculi (l) of the male and female articulate with the dorsal wall of the hypostome. In the male the point of articulation is just posterior to the region of modification. In the female the point of articulation is lateral to the lateral hypostomal seta. The corniculi are shorter (92 microns) in the female than they are in the male (104 microns). In both sexes they resemble slender blades which curve slightly outward. From their medial surfaces is a lightly sclerotized extension with a serrated edge. In the female there are from twelve to fifteen serrations on its edge and in the male there are from eight to ten.

Chelicerae.—(Pl. I B, D) The three segmented chelicerae (a) of *E. latus* are very powerful structures. In the males and the females the second segment is the longest and the first and third are subequal. The chelicerae of the female, however, are longer and more slender than those of the male. The ornamentation, though the same on both sexes, is more pronounced in the female. The following description is applicable to the chelicerae of the male and female. The movable digit in most specimens usually has thirteen teeth plus a large tooth at its base which fits into a groove at the base of the immovable digit. From its medial surface project two large excrescences, both directed anteriorly. The more distal of the two follows the curve of the digit and has many fine serrations on its free surface. The other is more delicate and its border is deeply fringed. The synarthrodial membrane at the base of the movable digit is expanded and its edge is slightly serrated. The fixed digit of the second cheliceral segment in most specimens has eighteen teeth. It has no excrescences as does the movable digit. On its medial surface, however, extending from about the middle of the digit to its base is a long, narrow, fringed membrane. On the dorsal surface of the segment at the base of the digit is a small membranous flap. It is not a seta as in some forms. On the lateral, anterior surface of the second segment are three irregular rows of tiny, anteriorly directed teeth. The first cheliceral segment has no ornamentation and is subequal in diameter as the second segment.

Pedipalps.—(Pl. I G) Designating the trochanter as number 2, the following series of numbers represents the relative length of the palpal segments, from the longest to the shortest: 3:4:2:5:6. The trochanter has two slender setae projecting from its ventral surface, both with setules restricted to their tips. The more posterior of the two is about one and one-thirds as long as the others. The femur has five setae, one mediodorsal, one ventral and three dorsal. The mediodorsal seta is the shortest of the setae and the only one which lacks setules. The ventral seta is at the same level on the segment as the most posterior of the three dorsal setae. It is one of the longest of the setae on the femur and has fine setules on its dorsal, anterior surface. Of the three dorsal setae, the most posterior one is the shortest. It is very rigid and has more setules than the other two. The other dorsal setae curve anteriorly and both have setules. The more anterior of the two is the longest. The

genu has seven setae: two medial, one ventral, one lateral and three dorsal. The two medial setae are the shortest of the setae on the genu. They are subequal in length, very narrow and appear rigid. The ventral seta is the only seta on the genu which has setules and these are only at its tip. It is a very rigid seta and its distal end curves slightly anterior. The lateral seta is about as long as the most anterior of the dorsal setae and very slender. The three dorsal setae curve anteriorly, and the most posterior of the three setae is the longest of the setae on the genu. The tibia has at least fifteen setae: three medial, one ventral, six lateral, and five dorsal. The three medial setae lack setules, are very slender and among the shortest of the setae on the tibia. The ventral seta is the most robust of the setae on the tibia and one of the longest. It is the only tibial seta with setules. The setules are restricted to its tip. The lateral setae are all slender and among the longest of the tibial setae. The tarsal setae are all nude and slender. It is characterized by the two-tined seta on its medial surface. It has an additional twelve to fourteen setae. Of these approximately ten are arranged in a ring on its dorsal surface. They are all subequal in length. On its ventral surface is the longest of the tibial setae. Ventral to the two-tined seta on the medial surface is a long seta which curves sharply upward at the anterior third of its length. On the dorsal surface of the tibia is a long, slender seta which curves upward from its base.

PASSALACARUS SYLVESTRIS Pearse and Wharton, 1936

Gnathosoma.—The gnathosoma of *Passalacarus sylvestris* projects from the anteroventral surface of the oval-shaped idiosoma. It is round in shape and more delicate than the gnathosoma of *E. latus*. Unlike *E. latus*, the posteroventral margin of the gnathosomal ring is anterior to coxae I and II. There is no sexual dimorphism exhibited and the gnathosoma of both sexes is similar. As in *E. latus* the most dorsal row of hypopharyngeal teeth are very long and readily seen from a ventral view.

Gnathosomal base.—(Pl. I A′, C′) The gnathosomal base is characterized by a series of ridges on its lateral and ventral surfaces. There are three conspicuous ridges on its ventral surface which are bisected by the deutosternum. The two posterior ridges traverse the gnathosoma and are parallel with each other. The more posterior of the two is at the same level as the distal edge of the most prosterior deutosternal plate. The more anterior one is approximately at the same level as the distal edge of the third deutosternal plate. The more distal of the three ridges curves slightly anteriorly. It originates at the distal edges of the most anterior plate of the deutosternum. In the specimens examined, these ridges were more prominent in the male than in the female.

Deutosternum.—The deutosternum (u) of the female (A′) is 129 microns long. It is narrow posteriorly and gradually widens anteriorly. It has five series of plates, two restricted to the narrow portion and three in the wider, anterior portion. The two posterior plates have no ornamentation but the distal edges of the three anterior plates are serrated. The deutosternum of the male (C′) measures 126 microns long. It is the same as the female except that the distal edge of the more anterior of the deutosternal plates in its narrow portion is slightly serrated in most specimens examined and in the female it is usually smooth.

Gnathosomal setae.—The gnathosomal setae (w) of the female measure 49 microns long and have approximately twelve setules. The setae of both sexes arise at the level of the second ridge on the gnathosomal base. The setae of the male measure 67 microns long and have approximately eighteen setules.

Horizontal plate.—(Pl. II C′) The horizontal plate of *P. sylvestris* is more delicate than that of *E. latus* and does not extend as far into the idiosoma as does that of *E. latus*.

Subcheliceral plate.—The bars of the subcheliceral plate (d) measure 150 microns long. They project into the propodosomal portion of the idiosoma. The bars do not arch outward as in *E. latus* but the distance between them gradually narrows posteriorly. The bridge which connects them posteriorly curves ventrally.

Epistome.—The epistome (i) of *P. sylvestris* is about three times wider than that of *E. latus*. The anterior third of the plate is more heavily sclerotized than its posterior two-thirds. The labrum projects from the central portion of the more heavily sclerotized portion.

Tentorium.—The tentorium (m) is similar to that of *E. latus*.

Cheliceral sheaths.—The cheliceral sheaths, their insertion and origin are similar to those of *M. floridanus*.

Pharynx.—The pharynx is simila· to that of *E. latus*.

Tectum.—(Pl. I E′, F′) The tecta of the male and of the female of *P. sylvestris* are the same. Its general contour and ornamentation are similar to that described for *E. latus*. In addition to the numerous rows of teeth on its dorsal surface, the tectum of *P. sylvestris* has many fine striations which radiate from the rows of teeth to the periphery of the tectum. The rows of teeth are not as pronounced as those of *E. latus*. On the ventral side of the tectum, the keel and the tooth are present. The tip of the tectum just anterior to the tooth is more heavily sclerotized than its sides. The tectum of the female measures 243 microns from tip to base and 203 microns at its widest portion; that of the male measures 252 microns from tip to base and 212 microns at its widest portion.

Epipharynx.—Pl. II B′; Pl. III A′-C′) The epipharynx (j) of *P. sylvestris* is similar to that of *E. latus*. The spines on its dorsolateral walls are longer but the degree of sclerotization of the ventrolateral walls and its general overall contour differ little from that of *E. latus*. The epipharynx of the female and the male measures 113 microns long.

Labrum.—(Pl. II B′, C′; Pl. III A′) The labrum (h) projects from the center of the epistome. It can be differentiated into two parts. A posterior, basal portion, which is contiguous with the epistome, posteriorly, and contiguous with the epipharynx, ventrally, is round in contour and from a dorsal view appears rather membranous. Projecting from the distal surface of this basal portion are four lancet-shaped structures. The most dorsal is the smallest (9 microns). Ventral to this single, dorsal projection are three similar processes. The central one of these is the longest and measures 30 microns. It has two, small teeth projecting from its dorsal surface. The two lateral processes are subequal in length (18 microns).

Hypopharynx.—(Pl. II A′; Pl. III A′-C′) The hypopharynx (q) of *P. sylvestris* is similar to that of *E. latus* and will not be described here. The hypopharyngeal teeth (g) which radiate on either side of the protosternum are also similar to those of *E. latus*.

Hypopharyngeal style.—(Pl. II A′, C′; Pl. III A′-C′) The hypopharyngeal styli (v) of *P. sylvestris* are longer and more slender than those of *E. latus* and recall those of *M. floridanus*. They are rather bulbous proximally and taper to a narrow point. Their entire surface is covered with tiny spines. They measure 155 microns in the female and 77 microns in the male.

Hypostome.—(Pl. I A′, C′) The hypostomal region (k) of the male and the female are similar. The medial walls of the hypostome are contiguous with the proximal portion of the protosternum; their lateral walls, however, are free. Other than the hypostomal setae, the hypostome has no ornamentation.

Hypostomal setae.—The three hypostomal setae are arranged so that each occupies the angle of a triangle, the longest side of which connects the distal and the lateral setae. The distal, medial and gnathosomal setae if connected would be on the locus of a straight line. The hypostomal setae are very delicate and slender. In the female the medial setae are the longest (92 microns) and have just a few setules. The lateral setae (64 microns) have the greatest number of setules. The distal setae (52 microns) are the shortest and lack setules. The hypostomal setae of the male are similar to those of the female. The length of the distal, medial and lateral setae of the male is 55, 86, and 70 microns, respectively.

Protosternum.—(Pl. I A′, C′; Pl. III B′, C′) The relationship between the protosternum (y) and the apodemes (r) which lend support to the lateral walls of the hypopharynx is the same as in *E. latus*. It measures 92 microns tall in the female and 89 microns tall in the male.

Hypopharyngeal processes.—(Pl. I A′, C′; Pl. II A′, C′) The hypopharyngeal processes (o) of *P. sylvestris* differ markedly from those found in *E. latus*. They are long, flat, flexible apophyses which extend distally from the apodemes of the hypopharynx. They measure 86 microns in the female and 77 microns in the male. Their medial surfaces are slightly serrated.

Hypostomal processes.—(Pl. I A′, C′; Pl. II A′, C′) The hypostomal processes (p) are smooth, slender, transparent structures which curve medially. They originate from the distal edge of the dorsal wall of the hypostome and project between the distal hypostomal setae and the corniculi. They are 55 microns long in the female and 61 microns long in the male.

Corniculi.—(Pl. I A′, C′; Pl. II A′, C′; Pl. III A′, B′) The corniculi (l) are heavily sclerotized, smooth, tooth-like structures which articulate with the dorsal wall of the hypostome. They project between the hypostomal processes and the lateral hypstomal setae. In the female they measure 70 microns and in the male 77 microns.

Chelicerae.—(Pl. I B′, D′) The slender, three-segmented chelicerae of *P. sylvestris* are delicate structures. The first segment of the chelicerae is the smallest and has no ornamentation. The second segment is similar to that of *E. latus*. The immovable digit has twelve teeth in the female. The most

posterior of these teeth is not on the cutting edge of the digit but arises from its lateral surface. It is the largest of the teeth and fits into a groove on the medial surface of the movable digit, just posterior to the most posterior tooth of the movable digit. At the base of the immovable digit on its dorsal surface is a short seta. On its medial surface is a fringed membrane similar to that in *E. latus* and on its lateral surface is a single row of tiny teeth. The movable digit of the female has eleven teeth, the most posterior of which is the largest of the teeth on either digit. It arises from the medial surface of the digit and would appear to fit into a groove on the medial surface of the immovable digit. As in *E. latus* there are two conspicuous excrescences which arise from the posterior half of the medial surface of the movable digit. The more anterior of the two is split in two, long, slender, filiform structures which are fringed distally. The posterior excrescence splits into a series of finger-like projections, the edges of which are also fringed. The synarthrodial membrane at the base of the movable digit is greatly expanded. The chelicerae of the male are shorter and more robust than those of the female. The number of teeth on each of the digits is about the same as in the female. The two excrescences on the movable digit differ from those of the female. They arise more posteriorly and each seems to arise from opposite sides of the digit. One excrescence, from the medial surface, resembles a spoon with its concave surface curved ventrally. The other excrescence arises from the lateral surface and is similar to the more posterior excrescence on the chelicerae of the female in *E. latus*. It resembles a needle with deeply fimbriated edges. Both of these excrescences extend about three-fourths the length of the movable digit.

Pedipalps.—(Pl. I G′) The relative size of the segments of the palps is as follows: 3:4:5:2:6. The trochanter has two nude setae projectng from its ventral surface. They are subequal in length. The dorsal, distal edge of the trochanter is interrupted with approximately five teeth. The femur has five setae, one mediodorsal, one ventral, and three dorsal. The mediodorsal seta is the shortest and lacks setules. The other four have setules. The ventral seta is among the longest of the setae on the femur. The most posterior of the three dorsal setae is approximately at the same level as the ventral seta. It and the most anterior of the dorsal setae are subequal in length. The central, dorsal seta is slightly shorter than the other two and curves anteriorly. The genu has seven setae, two medial, one ventral, one lateral and three dorsal. The two medial setae are nude and the shortest of the setae. They are subequal in length and curve dorsally. The ventral seta is a relatively long seta, rather rigid and curves anteriorly at its tip. Its ventral surface has many setules at its tip. The lateral seta is long, rigid, nude, and projects anteriorly. The most posterior of the three dorsal setae is the longest of the setae on the genu and the only seta from the dorsal surface with setules. The other two dorsal setae are subequal in length and both curve anteriorly. The tibia has at least sixteen setae, three medial, one ventral, six lateral and six dorsal. They are all nude. The three medial setae are among the shortest of the tibial setae. The most vertral of the three is the smallest of the tibial setae and is very narrow and rigid. The ventral seta is one of the longest of the setae. The lateral setae are subequal in length. The dorsal setae range in size from short, anteriorly, to long, posteriorly. One of the dorsal setae near the posterior end curves sharply anteriorly. The tarsus is characterized by a three-tined seta

(G″) on its medial surface. There are two tall tines and a shorter one. The taller tines are subequal in length and about five times longer than the shorter one. The short tine is the most ventral in position. The tarsus has an additional twelve to fifteen setae. About ten or eleven of these are arranged in a ring on the dorsal surface. They are all slender and subequal in length. There are two long setae from its ventral surface, one from its lateral surface and one from its dorsal surface. All setae on the tarsus are nude.

DISCUSSION

The masterful piece of work done by Oudemans in 1928 is indeed startling when one considers that he made no real dissections of the gnathosoma but only managed to press the specimens between the cover slip and the slide. He knew of no internal skeleton of the gnathosoma which divides it into dorsal and ventral components or of the muscles which insert within epipharynx. He understood, however, the relationship of the other mouth structures and drew them so clearly in the specimens he studied that there is little difficulty in applying our terminology to the forms he figured. The one exception to this is a slender, tapering, tongue-like structure he pictures ventral to the epipharynx in the two representatives of the Diplogyniidae. He called it a hypopharynx and it is labeled as the hypopharynx (q) in plate II, F, G. From its position, however, it is more likely the protosternum, although one cannot be certain until his material is studied.

Oudemans (1914) in a paper on the mouth parts of the Acari called the "unpaired, median, flask-shaped organ which closes the mouth dorsally" (*Het labrum = het onparige mediane dolkvormige orgaan, dat den mond dorsaal alfsluit*) the labrum. In his 1928 paper on the Diplogyniidae, Oudemans does not use the term "labrum" for any structure but labels the structure he defined as the labrum in his 1914 paper as the epipharynx. The reason for this change is not given, but the structure to which the term is referred in 1928 is the epipharynx as used now. The term "epipharynx" as used by Oudemans in 1914 refers to a "pair of membranous organs near the labrum plus the styli" (*De epipharynx = de parige membraneuse organen naast het labrum + de styli.*). He suggested for the paired membranous organs the term paralabra and retained the term styli. (*Ik stel voor ze paralabra te noemen, terwiji de naam styli gevoegelijk behouden kan blijven.*) It is not understood for what his term "styli" stands unless it could refer to the salivary styli found in some forms. The structures designated as the "paralabra" by Oudemans are the hypopharyngeal styli.

Oudemans' interpretation of the gnathosoma of *E. ovale* is not as clear as that of *D. tropica* and *D. indica*. He had difficulty in homologizing the structures of *E. ovale* with those of *D. tropica* and *D. indica*. His study of the male rather than the female was probably responsible for this difficulty, since the gnathosoma of the males in the family Euzerconidae are greatly modified.

It might be added that recent workers who have attempted to use the terms employed by Oudemans on the gnathosomal structures of parasitic forms necessarily meet with some difficulty since the forms which Oudemans studied possessed large, shear-like chelicerae that are characteristic of many predaceous forms. The ease with which Oudemans' interpretations and the present study

complement each other is because representatives of the same families were investigated.

The feeding appartus of the Euzerconidae and the Diplogyniidae recalls that of *Megisthanus floridanus*, a Megisthanina, as reported in a recent paper by Gorirossi and Wharton (1953). The same complex of structures are present in their respective positions. The main difference between them is one of degree of development and lies in the relation between the protosternum and the hypostome. In *M. floridanus* the lateral walls of the protosternum are contiguous with the medial walls of the hypostome. In the present species, on the other hand, the protosternum projects freely between the hypostome and forms the groove which protects the hypopharyngeal walls. The hypopharyngeal dilator muscles which originate from the walls of the hypostome are not as extensive in *E. latus, D. indica* and *D. tropica* as they are in *M. floridanus*.

Structures which are thus far peculiar to the Celaenopsina and to the Euzerconidae in particular are the epipharyngeal styli. They are located just dorsal to the epipharynx and lateral to the labrum but have been designated as epipharyngeal styli because they do not appear to originate from the epistome as does the labrum; also, they are of a completely different texture than the labrum. The Euzerconidae are curious also insofar as the hypostomal region of the gnathosoma is concerned. Whereas the gnathosoma of the female is typically mesostigmatid in structure, the gnathosoma of the male is secondarily modified, probably for sexual purposes. Oudemans, who figured a male in his 1928 paper, referred to the modification as being almost teratological. The modification of the gnathosoma, however, suggests several interesting speculations concerning the derivation of the gnathosomal elements. It will be recalled that in the male the region designated as the gnathosomal base is delineated from the rest of the gnathosoma by membranes, while the palpal coxae are associated with the mouth parts. Of course, nothing of the embryological anlage can be deduced from the purely morphological study presented here. However, the facts support the hypothesis that the hypostome is in reality a modified palpal coxopodite, while the gnathosomal base, i.e., that portion associated with the deutosternum and which bears the gnathosomal setae, probably arises from a part of the idiosoma. This question has been debated by many early workers who were interested in homologizing the mouth parts of the Acarina with those of the Arachnoidea. It can only be resolved by embryological study.

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LIST OF ABBREVIATIONS

A—chelicera. A′—internal cheliceral sheath. A″—external cheliceral sheath. B—tectum. C—tooth on ventral wall of tectum. D—subcheliceral plate. E—palp. F—epipharyngeal stylus. G—dorsal row of hypopharyngeal teeth from lateral membrane of apodeme (*Paralabra externa*). H—labrum (*Zuerst eine mediane kurze Schleife, ventral davon zwei submediane, sehr breite und kurze, hyaline Lappen, welche selbst noch eine*

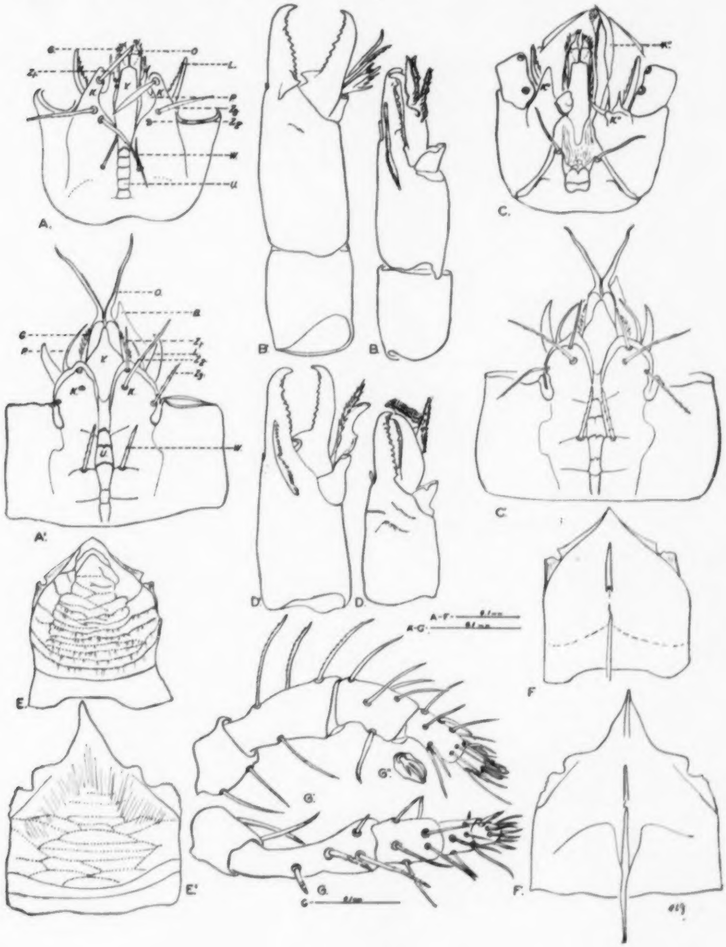

PLATE I

A.-G. *Euzercon latus;* A′-G′. *Passalacarus sylvestris;* A., A′. Ventral view of gnathosoma of female; B. Medial view of chelicera of female; B′. Lateral view of chelicera of female; C. Ventral view of male, note hypostomal modifications; C′. Ventral view of male; D. Lateral view of chelicera of male; D′. Medial view of chelicera of male; E., E′. Dorsal view of tectum; F., F′. Ventral view of tectum; G. Palp; G′. Palp, lateral view; G″. Three-tined seta on palpal tarsus of *P. sylvestris*, medial view.

submediane Schleife haben). I—epistome. J—epipharynx (*dann wieder ventral davon, eine lange, platte, schmale Schleife; und endlich der proximal breite, distal sich stark verjüngende Epipharynx*). J′—epipharyngeal base. K—hypostome. K′—dorsal wall of hypostome. K″—hypostomal modifications in male *E. latus*. L—corniculus. M—tentorium. N—epipharyngeal muscles. O—hypopharyngeal processses. P—hypostomal processes.

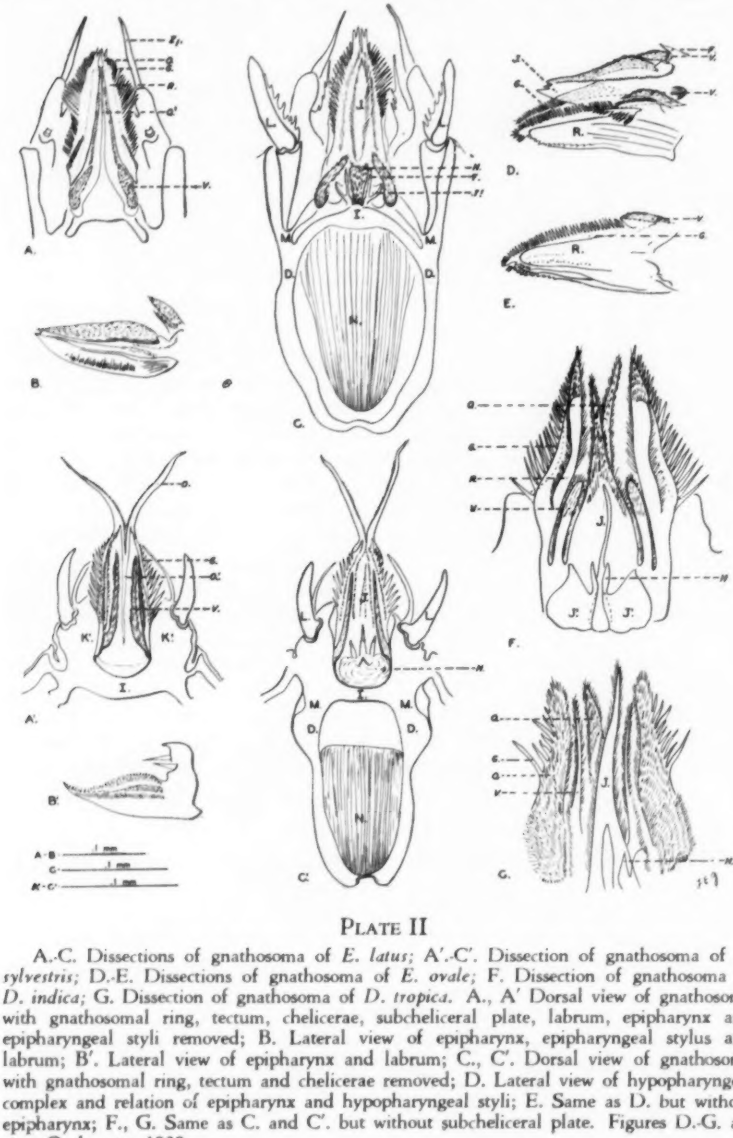

PLATE II

A.-C. Dissections of gnathosoma of *E. latus;* A′.-C′. Dissection of gnathosoma of *P. sylvestris;* D.-E. Dissections of gnathosoma of *E. ovale;* F. Dissection of gnathosoma of *D. indica;* G. Dissection of gnathosoma of *D. tropica.* A., A′ Dorsal view of gnathosoma with gnathosomal ring, tectum, chelicerae, subcheliceral plate, labrum, epipharynx and epipharyngeal styli removed; B. Lateral view of epipharynx, epipharyngeal stylus and labrum; B′. Lateral view of epipharynx and labrum; C., C′. Dorsal view of gnathosoma with gnathosomal ring, tectum and chelicerae removed; D. Lateral view of hypopharyngeal complex and relation of epipharynx and hypopharyngeal styli; E. Same as D. but without epipharynx; F., G. Same as C. and C′. but without subcheliceral plate. Figures D.-G. are after Oudemans, 1928.

Q—hypopharyngeal wall [*den ganz ventralen Hypopharynx (wohl ein mediodorsaler Anhang des Hypostoms)*]. Q′—hypopharyngeal groove. R—apodeme (*welche dorsal noch einen Längslappen als Anhang tragen, alles am Rande gefranst, selbst distal allseitig gefranst*). R′—lateral covering of apodeme. S—pharynx. T—pharyngeal constrictor muscles. T′—pharyngeal dilator muscles from gnathosomal ring. T″—pharyngeal dilator muscles from epistome. U—deutosternum. V—hypopharyngeal stylus, (*Paralabra interna*). W—gnathosomal seta. X—hypopharyngeal dilator muscles. Y—protosternum. $Z_{1, 2, 3}$—distal, medial, and lateral hypostomal setae.

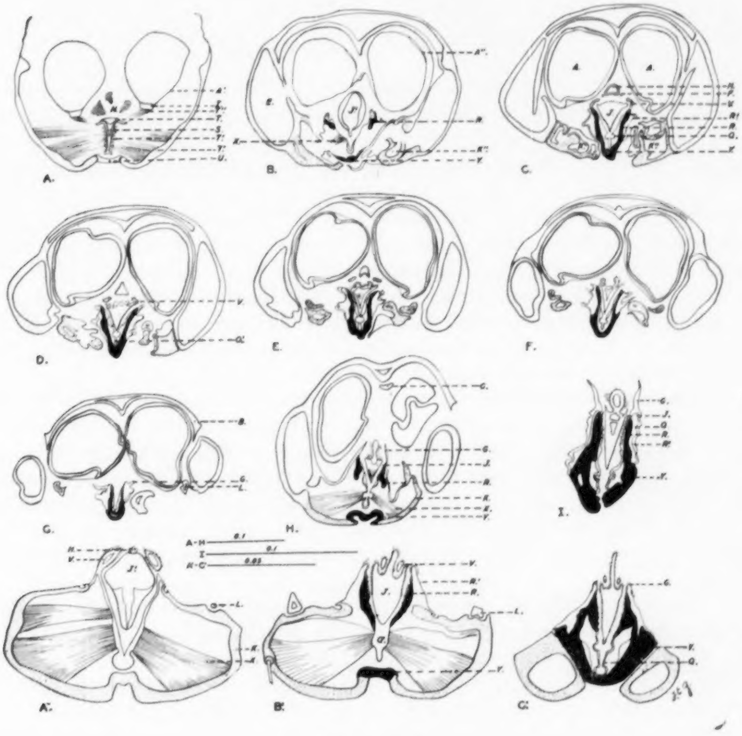

PLATE III

A.-G. Transverse sections of gnathosoma of male *E latus* from posterior to anterior end; Figures H., I. Transverse sections of gnathosoma of female *E. latus*. I. Magnified portion of apodemal-protosternal complex; Figures A′.-C′. Transverse sections of gnathosoma of female *P. sylvestris* comparable to Figures B., H. and I. of *E. latus*. In all figures the strippled portion represents sclerotized regions of the hypostome and the solid portion represents the apodeme and the protosternum. All sections were cut at eight microns. A. At level of epistome; B. At level of origin of hypopharyngeal styli; C. At level of epipharyngeal styli; D.-G. Illustrate gradual change in contour of structure from level of labrum to corniculi; H. At junction of apodemal-protosternal complex and hypostome; I. Detail of apodemal-protosternal complex, note similarity to hypostome of ticks.

Lampreys in the Lake Champlain Basin

Francis H. Wilson
Lebanon Valley College, Annville, Pa.

Lampreys have probably been in Lake Champlain as long as there has been a Lake Champlain. The earliest actual report is by DeKay (1842) who named and described *Ammocoetes unicolor* on the basis of larvae sent to him by Zadock Thompson of Burlington, Vermont. The present status of Dekay's species is uncertain.

In his *History of Vermont*, Thompson (1853) mentions two lampreys One he refers to as *Ammocoetes concolor* Kirtland and states it was collected from Winooski River during the drought in September 1841. The other he calls *Petromyzon nigricans* LeSueur and uses the common name blue lamprey. The exact locality is not given. He writes of it as being five inches long and mentions this species as found attached to fish when caught in a seine. He states that it seldom exceeds six to eight inches in length. The description suggests the freshly metamorphosed lake lampreys now known as *Petromyzon marinus* L., although one wonders that he did not mention finding the larger, more nearly mature individuals. In this 1853 publication, peculiarly enough, he does not mention the larvae he had sent to DeKay, which were described by DeKay under the name *Ammocoetes unicolor*.

The next references to Champlain lampreys are by Greeley in 1930. He lists two lampreys; the northern or silver lamprey is stated to be "moderately common in Lake Champlain." It was reported spawning in Putnam Creek at Crown Point and larvae were found in the mud and sand. One larva was also found in the lower part of Ausable River. In this survey the lake lamprey is similarly listed as "moderately common." Adults were reported attached to fish and larvae identified as *Petromyzon marinus* L. were found in Putnam Creek.

The above summarizes the published information on lampreys in the Champlain area and serves as a background for the present study.

Since 1950 the streams on the New York side from Crown Point to and including the Little Chazy were examined for lampreys either for the spawning adults, nests, or larvae depending on the season of the year. Lampreys were found in Putnam Creek, Little Ausable and Salmon rivers which were excellent breeding areas with moving water over suitable gravel beds, though the breeding areas are restricted to their lower portions because of falls over which the lampreys are unable to pass. All of the other streams in this area are either temporary or else have falls which prevent the lampreys from reaching the gravelly portions of the stream-bed. Other streams, such as Scomotion Creek and the lower part of the Little Chazy, are too sluggish for lampreys. In the upper part of the Little Chazy lack of gravel and extensive bedrock appears to be the discouraging factor.

Salmon River was selected as the most convenient spot at which to study breeding activities of lampreys in the region. It flows into Lake Champlain about four miles south of Plattsburg. A sandbar about two hundred yards east of Route 9 marks its entrance into the Lake. About one hundred yards west of

Fig. 1.—Bedrock outcrop with downstream dip on Salmon River about 100 yards west of route 9. (Photograph by Robert H. Quinn)

Route 9, a bedrock outcrop dips downstream so that the water in dropping about six feet fans out over this bedrock as shown in figure 1. At South Plattsburg a series of bedrock outcroppings and a five foot fall makes an impassable barrier for the lampreys. In this two mile distance from Route 9 to South Plattsburg, the river winds and oxbows to form a waterway of nearly five miles and much of this area is ideal for spawning and for the development of the larvae.

It is not necessary to construct a weir or use traps of any kind in order to study the spawning runs up this river. The bedrock outcroppings near Route 9 forms a barrier over which the lampreys pass with difficulty. The water is too swift for them to travel by continuous swimming. They swim up a short distance and attach to the rocks with their mouths and after resting swim another short distance upwards and attach again, repeating this process until they are over the barrier. This barrier is about fifty feet wide and shallow water at the edges gives the smaller lampreys (brook and northern) an opportunity to pass up the barrier. The lake lampreys can pass up the barrier against the strong current at the center. It is possible with an electric lantern to examine this barrier at night when the lampreys are most active and in this shallow water to follow the activities of the lampreys and migrating fish. They can be easily caught in a dipnet. Rarely are lampreys seen in the daytime and at night they avoid a strong light, often detaching from the rocks and swimming away.

In the spring of 1952 and 1953 weekly and often nightly visits were made to these rocks from March 28 to the middle of June. The visiting period was from 8-11 p.m. eastern standard time. In 1953 water temperatures were taken at 8 p.m. Portions of the river between Route 9 and South Plattsburg were examined weekly and on occasion nightly for signs of spawning activity.

The following descriptions summarize the observations made over this two year period.

Observations on the Lake Lamprey, *Petromyzon marinus* L.

Lake lampreys were first seen on the rocks on April 6 when the tempera-

ture at 8 p.m. was 46°F. Their appearance through April was irregular, apparently depending on temperature. If temperature was 50°F one could count on finding two or three. Their numbers increased as the temperature rose. The largest collection of the season was made on May 5 when the temperature was 58°F. One hundred twenty-three were collected from the rocks from 8 p.m. to midnight. During the next week the migration over the rocks tapered off rapidly. On May 12 with the water at 70°F only three were seen and the last one seen passing up the rocks was on May 28.

On May 10 lake lampreys had reached the barriers at South Plattsburg. Four were seen attached to these rocks so it can be assumed that they were now present throughout the breeding areas of the river.

On June 2, the areas where spawning usually took place were examined again but no lamprey nests were seen. However on the night of June 4 this same area showed nest construction going on at practically every riffle where suitable stones and gravel were available. By June 17 spawning activities had practically ceased, only one adult lamprey was seen and nests were showing deposits of fine sand.

Examination of nests on June 25 showed some nests with larvae, some with eggs and larvae, some with eggs only, and some with larvae apparently just hatched (6 mm long) as they were comparatively inactive and showed no tendency to burrow. A nest examined on June 26 showed very active larvae 7 mm long. When these were placed in the quiet water of a glass jar they sank or swam to the bottom and burrowed into the fine silt at the bottom of the jar. When they were shaken up in the bottle, they showed no tendency to swim and apparently *froze;* only when the water became quiet did their swimming begin. This behavior apparently is like their movement downstream. They drift in the flowing water and only start to drop to the bottom and burrow when they are carried into quiet areas or edges along the shore. Larvae are found in the silt and fine sand in which there is considerable organic matter. As they mature, they seem to prefer the coarser sand and gravel with less organic matter and often with roots of water plants growing through it. Freshly metamorphosed adults are found from the first week of September on through the fall. In 1951, thirty freshly metamorphosed adults were dug, the smallest was 133 mm long, and the largest 166 mm long. The thirty averaged 147 mm.

OBSERVATIONS ON THE NORTHERN OR SILVER LAMPREY ICHTHYOMYZON UNICUSPIS HUBBS AND TRAUTMAN

The northern lampreys were first seen ascending the bedrock barrier on the night of April 9 when the temperature at 8 p.m. was 54°F but only one was found. No more were seen until April 30 when the temperature again reached 54°F and 2 were found. Their upstream migration reached its peak on May 9 and 10 when the water reached 66°F and 20 were seen on each of these nights. The numbers dropped rapidly and for most of the rest of May only two or three were seen nightly. Two northern lampreys were collected on the nights of June 6, 7 and 9. The females were swollen with eggs and the slightest pressure would cause them to ooze from the genital pore.

Mating activities were not observed. On June 9, 1951, a nest was found with two lake lampreys and one northern lamprey busily at work and on June

25 a single male northern lamprey was seen in an old lake lamprey nest. This suggests that they may use the nests of the lake lampreys or else build one similar to it.

A decided color change was noticed during the spawning run. The earliest northern lampreys captured were yellowish to liver colored, but as the run progressed they became grayish and with a blue tint.

Larvae were not identified and no freshly metamorphosed adults were found.

OBSERVATIONS ON THE BROOK LAMPREY, ENTOSPHENUS LAMOTTENII LESUEUR

Brook lampreys were first seen ascending the rock barrier on April 6 when the temperature of the water was 46°F; two were seen. Brook lampreys were not seen again until the temperature of the water reached 50°F or above. The maximum number seen was on April 8 when the temperature was 52°F and thirty-eight were collected. On April 9 the water was 54°F and twenty-three were collected. They persisted irregularlyy into late May. A last collection of four was made on May 28. In the spring of 1952 over two hundred fifty specimens were collected and in 1953 one hundred fifty were collected. Like the northern lamprey they ascend the barrier in the shallow water at the extreme ends of the rock barrier.

Their spawning beds were not found. Salmon River was examined at every spot that seemed at all favorable for spawning from April 12 to early in June and several times the entire river to South Plattsburg was examined both at night and in the daytime. It would seem that Salmon River must have contained hundreds of adult brook lampreys if the number collected is any index at all.

The large number ascending the barrier near Route 9 could be explained if the adults had been washed down to the lake by the early spring floods or if the larvae had been washed down at other high water periods and had developed in the sand below this barrier or in the sandbar across the mouth of the river. Numerous lamprey larvae have been found in this area although no attempt was made to identify them. There are no nearby streams from which they could be washed out, or from which they could make their way to Salmon River by way of the lake. Surface (1899) reports that the brook lampreys do not have a spawning run but spawn in the same area in which they become adults. Thus the spawning run of the brook lamprey in Salmon River seems to be unique. Their occurrence in the lower end instead of the upper branches of the river is also unusual since most reports place the brook lampreys in the upper reaches of streams.

Two hundred adults were measured. The smallest was 135 mm in length and the longest was 179. The average length was 157 mm.

These are the first adult brook lampreys to be reported from the Lake Champlain basin. Vladykov (1949) reports the presence of this brook lamprey in the Richelieu River on the basis of a single ammocoetes. He reports adults and ammocoetes of the northern brook lamprey *Ichthyomyzon fossor* Reighard and Cummins from the Yamaska River which is just east of the Richelieu, but as yet it has not been found in the Lake Champlain drainage basin.

EFFECTS OF DRY WEATHER ON LARVAE AND METAMORPHOSING ADULTS

Conditions of rainfall in the summer and fall of 1950 and 1951 were considered to be normal but there was little rain during the late summer and fall of 1952 and a marked effect was shown on the distribution and numbers of ammocoetes and young adults. In July of 1952 larvae of all sizes were found as usual throughout the sands of the Salmon River breeding areas. In early August they were difficult to find in the area above Route 9 and the gravel was becoming slimy and the deposits of vegetable matter were rotting noticeably. In late August they had all but disappeared from these sand deposits where in the two previous years they had been abundant. Early in September examination of the sand and silt deposits between Route 9 and the lake showed ammocoetes of all sizes in abundance, so plentiful that two hundred were collected in an hour of digging and freshly metamorphosed adults of both *Petromyzon marinus* L. and *Entosphenus lamottenii* (LeSueur) were found. In previous years this area had been a relatively poor collecting area. Their abundance suggested that with the reduction in stream flow there had been a heavy migration toward the lake. Larvae and adults continued to be abundant in this area until November when floating dead larvae were noticed and notochordal remains were dug up. It became almost impossible to find living ones by digging in the area where a month before they had been so numerous. In digging it was noticed that decomposition of the underlying vegetable remains had become very active, noticeably releasing marsh gas. Walking and digging would release quantities of bubbles to rise up through the water. While no work was done to determine how toxic marsh gas is on the larvae, nevertheless the disappearance of live larvae was definitely associated with the appearance of marsh gas in this area where water was actively moving and the surface sand and silt appeared in otherwise good condition for lampreys.

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The Fishes of Blue River in Oklahoma with Descriptions of Two New Percid Hybrid Combinations[1]

Allan D. Linder

Oklahoma Agricultural and Mechanical College, Stillwater

The fishes of Blue River in Oklahoma have received very little attention from ichthyologists. The early collectors apparently by-passed Blue River completely. Paden (1948) reported *Microperca* (= *Etheostoma*, in part) *microperca* (Jordan and Gilbert) from Thomas Bricken Spring, a tributary of Blue River and Hubbs and Bonham (1951) reported *Notropis blennius* (Girard) from the same locality. Moore and Rigney (1952) described *Poecilichthys* (=*Etheostoma*, in part) *radiosus cyanorum* from Blue River and included some notes concerning the percid associations in the river. Since there are so few references to the fish fauna of Blue River, an annotated list seems pertinent.

Two new percid hybrid combinations, collected and identified by Dr. G. A. Moore of Oklahoma Agricultural and Mechanical College, are described. The combination *Etheostoma radiosum cyanorum* (Moore and Rigney) × *Etheostoma spectabile* (Agassiz) subsp. was taken from Blue River 24 miles south of Ada, Oklahoma. The hybrid, *Etheostoma spectabile pulchellum* (Girard) × *Etheostoma whipplei whipplei* (Girard), is included because of the close relationship of the parental species of it and those of the above-mentioned hybrid. The latter specimen was taken from Sand Creek near Foraker in Osage County, Oklahoma.

Description of the river.—The Blue River rises in Pontotoc County, Oklahoma, about six miles west of Fittstown. It is about 100 miles long, drains an area of approximately 660 square miles and flows in a southeasterly direction through Pontotoc, Johnston and Bryan counties to join the Red River south and east of Durant. The watershed is composed entirely of gently rolling hill country, about 48 per cent of which is timbered. Elevations at the headwaters are about 1250 feet above sea level, decreasing to approximately 500 feet above sea level near the river's mouth. The average annual rainfall varies from 37 inches at the headwaters to 40 inches at the lower end of the basin. The overflow area is rather narrow and, in the lower 60 miles of the river, approximately 12,000 acres are subjected to overflow annually (Anon. 1936). The Blue River is a clear and moderately swift stream with an average gradient of about 7.5 feet per mile. The native vegetation of the entire watershed is a typical oak-woods association.

List of collections.—The collections, with dates and localities, are given in chronological order and are followed by a description of collection stations.

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[1] Contribution from the Research Foundation and (No. 197) from the Department of Zoology, Oklahoma Agricultural and Mechanical College, Stillwater. Prepared under the direction of George A. Moore. The writer is indebted to Drs. R. W. Jones, F. M. Baumgartner and I. E. Wallen for criticisms of the manuscript.

The symbols (1a, 1b, 2, etc.) refer to collections by Moore and parties and are used in order to avoid long and frequent repetition in the annotated list.

Station 1a, July 21, 1946.—Thomas Bricken Spring in T1S, R6E, Johnston County, 24 miles south of Ada by the bridge on Highway 99. A small concrete dam was constructed below the spring, which is now submerged by the impounded water that overflows to form a small creek about 100 feet in length. The bottom of the creek consisted of rock, gravel and sand. Considerable water cress, algae and *Polygonum* sp. were found below the dam but were not very abundant farther downstream. This station and the following are situated very close together but are separated because of great contrast in habitat and fish populations.

Station 1b, July 21, 1946.—Blue River T1S, R6E, Johnston County, 24 miles south of Ada by the bridge on Highway 99. Here the river flowed over an outcrop of limestone which produced a rocky and gravelly riffle between steep and heavily wooded banks. Very little aquatic vegetation was present. This is the type locality of *Etheostoma radiosum cyanorum* (Moore and Rigney).

Station 2, April 4, 1947.—Blue River near its source, in Pontotoc County, southwest of Ada. The river bed at this station was predominantly of fine sand and mud with some gravel and rocks. Aquatic vegetation was almost entirely lacking.

Station 3a, April 5, 1947.—Thomas Bricken Spring (see 1a).

Station 3b, April 5, 1947.—Blue River (see 1b).

Station 4, April 5, 1947.—Little Blue River in Johnston County, NW 1/4, S30, T1S, R7E; the Howard Smith Place, 1 1/2 miles due east of Connerville. The river bed consisted of sand, gravel and rocks, mostly of small size. This area was surrounded by a level flood plain. Aquatic vegetation was absent.

Station 5, April 6, 1947.—Blue River in Johnston County, 10 miles west of Wapanucka on Highway 7 and 3 miles south at Hughes Crossing. The stream bed consisted mainly of solid rock with, here and there, some sand and gravel. Water cress and *Spirogyra* sp. were abundant in the small springs and creeks leading to the stream. A small amount of *Vaucheria* sp. was found on the rocks in the river. There was a flat flood plain bounded by bluffs some distance from the stream. A total of 21 species, represented by 34 specimens, was taken at this station and records for three others were obtained from Mr. Hughes. The scarcity of specimens is in part explained by the difficulty encountered in seining operations over the irregular bottom, often strewn with large boulders.

Station 6*a*, April 14, 1949.—Thomas Bricken Spring (see 1a).

Station 6*b*, April 14, 1949.—Blue River (see 1b).

Station 7, *April* 15, 1949.—Cedar Creek in Bryan County, 7 miles east and 1 mile south of Durant on Old Highway 70. This fast-flowing creek had many riffles and small falls with deep pools below the latter. The stream bed consisted of rocks (covered with algae), gravel and sand. The surrounding area was open woods and prairie.

Station 8, April 15, 1949.—JN Creek in Bryan County, 8 miles east and 1 mile south of Durant on Old Highway 70. The bottom of this small creek consisted of sand, mud, and a little gravel. No aquatic vegetation was apparent; and the surrounding area contained typical oak-woods vegetation. Two

hundred and forty-seven specimens, representing 18 species, were collected here.

Annotated list.—Following the scientific and common names of each species, references, symbols referrring to collections, and pertinent data, if given, are in that order. Species are being reported as first records for the Blue River and its tributaries unless followed by references.

CLUPEIDAE

1. *Dorosoma cepedianum* (LeSueur). Gizzard Shad.

Although no specimens were collected, Mr. A. B. Hughes stated that this species has been caught at Hughes Crossing.

CATOSTOMIDAE

2. *Moxostoma duquesnei* (LeSueur). Black Redhorse.—5.

3. *M. erythrurum* (Rafinesque). Golden Redhorse.—1b, 3b, 4, 5, and 7.

The specimens collected from Little Blue River in April 1947 were in breeding color.

4. *Minytrema melanops* (Rafinesque). Spotted Sucker.—4.

CYPRINIDAE

5. *Notemigonus crysoleucas* (Mitchill). Golden Shiner.—2, 3a, 3b, 4 and 5.

6. *Chrosomus erythrogaster* Rafinesque. Southern Redbelly Dace.—1a and 3a.

7. *Hybopsis biguttata* (Kirtland). Hornyhead Chub.—3b and 5.

8. *Notropis percobromus* (Cope). Plains Shiner.—3b and 6b.

9. *N. rubellus* (Agassiz). Rosy Shiner.—8.

10. *N. f. fumeus* Evermann. Ribbon Shiner.—6b and 8.

This is believed to be the westernmost record for this shiner.

11. *N. umbratilis* (Girard). Redfin Shiner.—3b, 4, 7 and 8.

12. *N. cornutus isolepis* Hubbs and Brown. Southern Common Shiner.—1b, 3a, 3b, 4, 5 and 6b.

13. *N. blennius* (Girard). River Shiner. Hubbs and Bonham (1951).—3a.

A single specimen (probably an escapee from Mr. Bricken's holding pond) was collected below the dam at Thomas Bricken Spring.

14. *N. venustus* (Girard). Blacktail Shiner. 4, 5, 6b, 7 and 8.

15. *N. l. lutrensis* (Baird and Girard). Plains Red Shiner.—1b, 2, 6b, 7 and 8.

16. *N. boops* Gilbert. Bigeye Shiner.—1b, 2, 3a, 3b, 4, 5 and 6b.

17. *N. d. deliciosus* (Girard). Southern Sand Shiner.—1b, 2, 3b, 4, 7 and 8.

The specimens collected from Little Blue River in April 1947 were near the breeding stage.

18. *N. volucellus* (Cope). Mimic Shiner.—3a, 3b, 5 and 6a.

19. *Phenacobius mirabilis* (Girard). Suckermouth Minnow.—1b, 2 and 3b.

The females, collected from Little Blue River in April 1947, contained eggs in various stages of maturity.

20. *Dionda nubila* (Forbes). Ozark Minnow.—8.

A single specimen, in breeding color, was collected from JN Creek in April 1949. The occurrence of *Dionda* in the river is interpreted as a case of bait-bucket introduction.

21. *Hybognathus placita* Girard. Plains Minnow.—7 and 8.

22. *Pimephales promelas confertus* (Girard). Southern Fathead Minnow.—2 and 7.

This and the next species, collected from Little Blue River in April 1947, were in breeding color.

23. *P. notatus* (Rafinesque). Bluntnose Minnow.—1b, 2, 3a, 4 and 5.

24. *P. vigilax* (Baird and Girard). Parrot Minnow.—7 and 8.

25. *Campostoma anomalum: plumbeum* (Girard) × *pullum* (Agassiz). Stoneroller.—1a, 1b, 2, 3a, 3b, 4, 5, 6a, 6b and 7.

These specimens are regarded as intergrades on the basis that 43 counts yielded an average of 42.6 (38 to 48) scales around the body.

AMEIURIDAE

26. *Ictalurus furcatus* (LeSueur). Blue Catfish.

Although no specimens were collected, Mr. Hughes stated that this species (common in Red River) has been taken at Hughes Crossing.

27. *I. punctatus* (Rafinesque). Channel Catfish.—5.
28. *Ameiurus melas catulus* (Girard). Southwestern Black Bullhead.—2, 3a, 4 and 7.
29. *A. natalis* (LeSueur). Yellow Bullhead.—1a.
30. *Pilodictis olivaris* (Rafinesque). Flathead Catfish.—3b.

CYPRINODONTIDAE

31. *Fundulus notatus* (Rafinesque). Blackband Topminnow.—4, 7 and 8.

POECILIIDAE

32. *Gambusia affinis affinis* (Baird and Girard). Western Gambusia.—1a, 1b, 3a, 3b, 4, 5, 6a, 6b and 7.

CENTRARCHIDAE

33. *Micropterus punctulatus* (Rafinesque). Northern Spotted Bass.—1b, 3a, 4, 5, 6a and 6b.
34. *M. salmoides* (Lacépède). Largemouth Bass.—2.
35. *Chaenobryttus coronarius* (Bartram). Warmouth.—6b.
36. *Lepomis cyanellus* Rafinesque. Green Sunfish.—1b, 2, 3a, 3b, 5, 6a and 8.
37. *L. megalotis breviceps* (Baird and Girard). Oklahoma Longear Sunfish.—1b, 2, 3b, 4, 5, 6b, 7 and 8.
38. *L. humilis* (Girard). Orangespotted Sunfish.—2, 3a, 6b, 7 and 8.
39. *L. macrochirus* Rafinesque. Bluegill.—4, 7 and 8.
40. *Pomoxis* (sp.) Rafinesque. Crappie.

No specimens taken, but Mr. A. B. Hughes attested its presence at Hughes Crossing.

PERCIDAE

41. *Hadropterus scierus* Swain. Northern Dusky Darter. Moore and Rigney (1952).—5, 7 and 8.
42. *H. copelandi* (Jordan). River Darter. Moore and Rigney (1952).—1b, 3b and 5.
43. *Percina caprodes* (Rafinesque). Logperch.—1b, 3b, 4, 5 and 6b.
44. *Etheostoma chlorosomum* (Hay). Bluntnose Darter.—8.
45. *E. radiosum cyanorum* (Moore and Rigney). Blue River Orangebelly Darter. Moore and Rigney (1952, descr.).—1a, 1b, 2, 3a, 3b, 4, 5, 6a, 6b, 7 and 8.
46. *E. spectabile* (Agassiz). Orangethroat Darter. Moore and Rigney (1952).—3a, 3b and 6b.

This species is listed in the binomial because there is evidence that this form possibly represents an undescribed subspecies. It is not *E. s. pulchellum* of northern Oklahoma.

47. *E. gracile* (Girard). Slough Darter.—8.
48. *E. microperca* Jordan and Gilbert. Least Darter. Paden, (1948) Moore and Rigney (1952).—1a, 3a and 6a.

SCIAENIDAE

49. *Aplodinotus grunniens* Rafinesque. Freshwater Drum.—5.

HYBRID COMBINATIONS

1. *Ethestoma* (*radiosum cyanorum* × *spectabile* subsp.).—3a and 3b.

Two specimens of this combination were collected and are described below.

DESCRIPTION OF THE HYBRID COMBINATIONS

Methods.—All specimens used in this study were collected in Oklahoma and are deposited in the Museum of Zoology of the Oklahoma Agricultural and Mechanical College (OAM) (hybrid specimens in Museum of Zoology University of Michigan, UMMZ). The diagnoses are based on specimens collected from the same localities and of the same sex as the hybrids. Since there are but two examples of one combination and one of the other, it was decided that an average of counts and measurements taken from ten specimens

of each parent species of each hybrid would be sufficient material upon which to base this study.

All counts and measurements were taken by Linder and later checked by Moore. When significant differences were obtained the counts and measurements were repeated, according to the methods of Hubbs and Lagler (1947), until accordance was obtained. Some counts and measurements taken deviate from or are not mentioned by the above writers and are explained below.

The measurement of the distance from the origin of the dorsal fin to the occiput was made from the structural base of the first dorsal spine to the occiput.

Body width is the greatest width of the body exclusive of the pectoral fins.

The width of the premaxillary frenum is the distance between the anterior ends of the premaxillary grooves.

The distance from the union of the gill membranes to the pelvics was measured from the apex of the angle formed by the union of the gill membranes to the insertion of the pelvic fin.

The distance from the union of the gill membranes to the mandible was measured from the apex of the angle formed by the union of the gill membranes to the tip of the mandible.

Since the scales at the origin of the spinous dorsal are embedded and difficult to see, the count of the scales above the lateral line was made below the origin of the soft dorsal.

All scale counts were made on the left side of the fish and all measurements were taken from the right side. All measurements were recorded to the nearest tenth of a millimeter and computed by machine into thousandths of standard length, head length, soft dorsal length, body depth and caudal peduncle length.

Although the range of some of the characters of the parental species overlap, it was believed that if a random sample of the parental species was taken the average value would be of more significance than the range. Overlapping of characters is common in this species group (*whipplei, radiosum* and *artesiae*) (Moore and Rigney, 1952).

Some characters studied exhibited such small differences between the parental species that they were considered to be of little value, and therefore, only those counts and proportions which show more than four percent difference between the parental species were used. Other characters exhibited values which were beyond the range of either parent. Hubbs and Kuronuma (1942) ascribed certain extreme characters in hybrid flounders to heterosis. They also indicated that if there is a genetic tendency in both parental species toward the reduction of a certain character, hybridization will cause an additive effect and produce an extremely reduced character in the hybrid.

The hybrid index used in this study is the same as that used by Hubbs and Kuronuma (1942) in which the formula, $\frac{V_H - M_1}{M_2 - M_1} = P$, is used to determine the position of the hybrid.

Several characters exhibited by the hybrids are identical with those of one or the other parental species indicating a possible dominant influence of one

parent or the other. An aggregate of hybrid index values in each instance gave an average value of near exact intermediacy, but the individual character values tend to range from 0 to 100.

Although these high and low index values are poor to show intermediacy, they are regarded as important in that they show tendencies in the hybrids toward one parent or the other. This marked influence in the hybrids of both parents is believed to be strong evidence that the parental species have been correctly determined.

A review of recent work on hybrids shows an emphasis on the more or less exact intermediacy of the hybrid (Hubbs, Hubbs and Johnson, 1943; Hubbs, Walker and Johnson, 1943; Trautman, 1948). These workers also indicated that all hybrid index values should give an average of nearly exact intermediacy. Trautman (1948) obtained an average hybrid index value of 52.43 for an ameiurid combination and Hubbs, Walker and Johnson (1943), working

TABLE 1.—A brief color comparison of *Etheostoma spectabile pulchellum, Etheostoma whipplei whipplei* and the hybrid, *E.* (*s. pulchellum* × *w. whipplei*)

	pulchellum	hybrid	whipplei
Head	slate, orange on cheeks and gill membranes	light slate	greenish cheeks, no bright colors
Sides of trunk	black spots forming bars	bluish green bars	small red spots
Sides of caudal peduncle	reddish orange and black bars	bluish green bars	reticulated, red and black
Belly	gray	yellow-green, pale streak on mid-line	light orange on sides, milky-white mid-line
Fins (colors in order distad from base)			
Spinous dorsal	red, white, blue-green	reddish brown, orange-red, greenish to emerald-green	gray (with red spots), red, white, blue-green
Soft dorsal	grayish red, brown, white, blue-green	olive-brown, reddish, green	brown, brick-red, white, blue-green
Caudal	bluish gray, with black spotting	black and red, greenish yellow, red, white, olive-green	gray (with red spots), red, white, blue-green
Anal	green	red spots, green	reddish, white, blue-green
Pectorals	yellowish, black rays, clear membranes	yellowish olive	yellowish, clear membranes
Pelvics	blue-black, white	blue-green	green

with cyprinodonts, obtained average hybrid index values ranging from 42-66 and a grand average hybrid index value of 55. Hubbs, Hubbs and Johnson (1943) recorded a grand average value of 49 for catostomid hybrids.

Etheostoma (*spectabile pulchellum* × *w. whipplei*).—The hybrid (UMMZ 162607) is an adult male 61.5 mm in standard length collected on March 25, 1950 from Sand Creek, 3 miles east of Foraker, Oklahoma. [2] The specimens of the presumed parental species used, *E. s. pulchellum* (OAM 4226) and *E. w. whipplei* (OAM 4227), were collected at the same time and from the same locality as the hybrid. The value of 0 (M_1) has been assigned to *E. s. pulchellum* and 100 (M_2) to *E. w. whipplei.*

All specimens used are adult males with a range of standard length in *E. s. pulchellum* of 32.9 to 44.3 mm and in *E. w. whipplei* of 43.0 to 69.0 mm. The hybrid had been preserved in a weak formalin solution and refrigerated in the dark for two months when the color description was taken. The color description for *pulchellum* was taken from unpublished notes of Moore and that for *whipplei* from Hubbs and Black (1941) and Moore and Rigney (1952) (Table 1).

Twenty-five characters were found to be intermediate in this hybrid, giving an average hybrid index value of 51.7 (Table 2).

Fig. 1.—Intermediacy in shape of genital papilla of hybrid, *Etheostoma* (*spectabile pulchellum* × *whipplei whipplei*). *E. s. pulchellum,* right; *E. w. whipplei,* left; and the hybrid, center.

The hybrid also expresses intermediacy in the shape of the genital papilla (fig. 1).

The color description of the hybrid shows the direct influence of one or the other parent in most instances. The following color description was kindly taken by Doctors Milton and Mary Trautman.

Eye with blue-black pupil and dusky iris. Postorbital dorsal head surface, the darkest portion of head, a deep olive lightening toward the snout. The cheeks and opercles slate-colored, the former light and the latter darker. Ventral surface of the head light slate-color and without spots. A definite preorbital bar, about two-thirds diameter of pupil in width, extends from tip of snout, through nostril, to the eye. A pronounced "tear drop" of the same width extends vertically downward to angle of mouth. A short triangulate, intensely dusky, postocular spot located slightly below center of eye. Background body color, olive, darkest dorsally and grading progressively lighter over sides to belly. Eleven dark bluish green bars cross the sides; the first, immediately behind the head, extends obliquely downward to include the dark humeral spot and continues as an oblong greenish blotch at the pectoral base. The second bar, as wide as the length of the eye, and the most pronounced of any on body, begins on the back immediately before spinous dorsal and extends slightly obliquely backward and downward to the lower belly, but not quite across the midline. Three short saddle-like blotches beneath spinous dorsal; the posterior and anterior brokenly connected with continuing bars around the body. Three saddle-like bars beneath the soft dorsal continue almost unbroken around the body. Two vertical green bars alternate with two intense orange-red blotches, as in *Etheostoma variatum* Kirtland, one above and one below the lateral line on the caudal peduncle.

Ventral surface of body with distinct yellow-green cast with a pale streak on midline of belly.

Spinous dorsal with bars of reddish brown spotting on the interradial membranes, the

[2] Since this paper was prepared, a second male hybrid (52 mm, standard length) of this combination and essentially in agreement with the one herein described was taken by R. J. Ellis from Sand Creek at Osage Hills State Park on May 4, 1952.

TABLE 2.—Comparison of the *Etheostoma* (*s. pulchellum* × *w. whipplei*) *hybrid with* the parental species

Character	pulchellum Range (Average)	Hybrid Counts; Proportions	Hybrid Index	whipplei Range (Average)
Counts				
Spinous dorsay rays	9-11(10)	11	71.4	9-12(11.4)
Anal rays	8-9(8.7)	10	72.2	10-11(10.5)
Pored lateral-line scales	30-39(35.0)	48	65.9	50-62(54.7)
Total lateral-line scales	50-60(53.2)	59	43.3	65-72(66.6)
Scales above lateral line	5-7(6.2)	7	26.6	8-10(9.2)
Scales below lateral line	7-10(8.2)	10	36.7	12-15(13.1)
Scales around caudal peduncle	19-23(20.5)	26	50.9	29-33(31.3)
Proportions				
Standard length in mm	32.9-44.3(36.1)	61.5	....	43.0-69.0(52.7)
Thousandths of standard length				
Snout length	67-80(71)	70	10.0	55-70(61)
Caudal-peduncle length	248-274(258)	237	77.1	218-241(231)
Pectoral length	249-295(272)	244	58.1	212-237(224)
Pelvic length	206-240(230)	226	20.0	202-220(210)
Head depth	175-206(189)	180	31.0	151-168(160)
Distance from UGM* to mandible	125-167(147)	151	20.0	156-176(167)
Distance from UGM* to pelvics	151-180(173)	146	77.1	126-143(138)
Head length in mm	10.0-13.8(11.1)	18.5	....	12.9-20.5(15.4)
Thousandths of head length				
Distance from UGM* to mandible	409-529(475)	503	28.5	536-612(573)
Distance from UGM* to pelvics	474-590(540)	486	86.1	420-500(475)
Head depth	573-652(615)	600	23.0	536-579(550)
Soft dorsal length in mm	9.4-14.1(10.6)	20.0	....	12.7-22.0(16.1)
Thousandths of soft dorsal length				
Pectoral length	863-1020(926)	750	90.7	682-787(732)
Pelvic length	714-842(781)	695	92.4	629-725(688)
Snout length	216-266(242)	215	61.3	182-236(198)
Head depth	615-691(642)	555	76.3	490-563(528)
Body depth	670-766(726)	660	48.4	530-630(602)
Body width	412-504(462)	435	58.7	371-455(416)
Body depth in mm	6.5-10.5(7.7)	13.2	....	7.7-13.0(9.7)
Thousandths of body depth				
Caudal-peduncle depth	463-523(492)	553	51.7	552-625(602)
Body width	600-686(641)	659	14.7	640-770(690)
AVERAGE HYBRID INDEX	....	....	51.0	....

* UGM—Union of gill membranes.

most anterior being the smallest and becoming progressively larger posteriad. Above this basal bar is a deep orange-red band, about the width of eye, composed of triangular interradial blotches with the longest leg of the triangle parallel to the anterior spine and the opposite angle slightly above and touching the next spine. Above this red bar is a very light greenish bar abruptly merging into a distal bar of emerald.

Basal one-fourth of soft dorsal, brownish olive; above this a broad reddish band, confined to the interradial membranes, and covering at least one-half width of fin; the rays remain olive in the band. Above this broad red band is one of pale greenish yellow contiguous with the narrow, deep green border.

Caudal base mesially marked with an indistinct dark triangular spot anteriad to which are two bright red spots, about size of pupil, one above and one below the lateral line. Above these spots a greenish triangle and below them a greenish suffusion.

Anterior third of caudal fin greenish yellow followed posteriad by a vertical reddish bar about width of eye, then a whitish bar and an olive-green border.

Anal distally bright emerald green with the spines and soft rays more intense than the webbing, and basally, on one-third its width, a deep orange on all interradial membranes except that between the fourth and fifth rays.

Pelvics a deep blue-green with rays more intense than membranes. Pectorals rather uniform, centrally yellowish olive and peripherally slate-colored.

From the above color description the parental influence can be summarized as follows. The influence of *E. w. whipplei* is seen in the general coloration of the soft dorsal and caudal fins, the pale streak on midline of belly and the basal red of the anal fin. The influence of *E. s. pulchellum* is expressed in that the red bar of the soft dorsal diminishes in intensity proximad, the green color of the rudimentary caudal rays, a faint suggestion of streaking on the sides and the faintly orange throat (figs. 2, 3 and 4; and table 1).

Further influence of *E. s. pulchellum* is evident in the naked cheeks, opercles and breast. The presence of embedded scales on the nape of the hybrid may be interpreted as an *E. w. whipplei* influence, although *pulchellum* some-

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Figs. 2-4.—2. *Etheostoma whipplei whipplei*. Adult male (55.0 mm standard length), (from Moore and Rigney, 1952); 3. *Etheostoma* (*s. pulchellum* × *w. whipplei*). Adult male (61.5 mm standard length), from Sand Creek 3 miles east of Foraker, Oklahoma. 4. *Etheostoma spectabile pulchellum*. Adult male (44.3 mm standard length), locale as for fig. 3.

times has a scaley nape. The complete infraorbital canal (8 pores) in the hybrid indicates a definite influence of *whipplei* which averages 8.1 pores in the complete canals on each side. The so-called humeral scale is well developed in the hybrid and also in *whipplei*, but is barely discernible in *pulchellum*.

Etheostoma (*radiosum cyanorum* × *spectabile* subsp.).—Two specimens of this hybrid combination, a male (61.0 mm, standard length) and a female (54.5 mm, standard length), (UMMZ 162608), were collected from Blue River in south central Oklahoma on April 14, 1949. The female specimen, when dissected, revealed the presence of eggs of various sizes, some apparently mature. The date of collection and the presence of large ova suggest the possibility that the individual had begun spawning.

The specimens of the presumed parental forms used, *E. r. cyanorum*, (OAM 2913), and *E. spectabile* subsp., (OAM 2915, 2099, 1604), were collected from the same locality on the same and different dates. Since the

TABLE 3.—A brief color comparison of *Etheostoma radiosum cyanorum*, *Etheostoma spectabile* subsp. *and the hybrid*, *E.* (*r. cyanorum* × *spectabile* subsp.)

	cyanorum	hybrid	spectabile
Head	dorsally blue-green slate, cheeks and gill membranes orange	opercles and cheeks orange, gill membranes red	reddish brown dorsally, cheeks greenish, gill membranes orange
Sides of trunk	buffy olive suffused with orange below lateral line	black bars ventrally suffused with orange	black blotches forming bars
Sides of caudal peduncle	indistinct bars	greenish black and red bars	greenish black and red bars
Belly	orange	orange	red spots
Fins (colors in order distad from base)			
Spinous dorsal	brown and buffy olive, orange, white, green	red, white, dark green	brick-red, white, green
Soft dorsal	brown and buffy olive, orange, white, green	red, white, light green	reddish brown, white, green
Caudal	brown and buffy olive, orange, white, green	red spots, brown, red, brown, green	reticulated with black, red spots at base
Anal	orange, blue-green	red, green	red, green
Pectorals	blue-green, orange tips	red and orange	yellow
Pelvics	orange, pale tips	green	green, yellow

two specimens are of opposite sex and express sexual dimorphism in certain characters, it was considered advisable to analyze them separately. Therefore, the male specimen has been compared with males of the parental species and the female specimen with females of the parental species. Also, a comparison of both hybrids with males of one species and females of the other species and the reciprocal cross of this combination was made. In all instances the value of 0 (M_1) was assigned to *E. spectabile* subsp. and 100 (M_2) to *E. r. cyanorum*.

The color description of the male hybrid was taken in the field at the time of collection. The female was not recognized as a hybrid until later and therefore, no color description was available. The color description for *E. r. cyanorum* was obtained from Moore and Rigney (1952) and that for *E. spectabile* subsp. from unpublished notes of Moore taken from a specimen collected with the hybrid. (table 3; figs. 5, 6, 7, 8, 9 and 10).

The male hybrid, when compared with males of the parental species, gave an average hybrid index value of 57.5 and the female, when compared with females of the parental species gave an average value of 45.2. A grand average hybrid index value of 51.4 was obtained. (tables 4 and 5).

The squamation of the male and female hybrids suggest influences of

TABLE 4.—Comparison of the male hybrid, *Etheostoma* (*r. cyanorum* × *spectabile* subsp.), with male specimens of the parental species

Character	cyanorum Range (Average)	Hybrid Counts; Proportions	Hybrid Index	spectabile Range (Average)
Counts				
Pored lateral-line scales	40-51(47.1)	43	53.4	35-41(38.3)
Unpored lateral-line scales	4-13(7.9)	11	51.6	12-16(14.3)
Scales below lateral line	11-13(11.7)	10	55.3	6-9(7.9)
Scales around caudal peduncle	26-29(27.2)	25	62.7	19-23(21.3)
Proportions				
Standard length in mm.	52.5-66.4(60.5)	61.0	....	38.4-54.5(43.2)
Thousandths of standard length				
Caudal-peduncle length	212-248(228)	238	65.5	247-271(257)
Soft dorsal length	306-354(333)	328	87.9	275-321(299)
Distance from UGM* to mandible	148-181(165)	159	75.0	123-165(141)
Head length in mm.	14.9-19.7(17.7)	18.5	....	11.5-15.3(12.6)
Thousandths of head length				
Distance from UGM* to mandible	492-602(564)	524	50.0	422-550(484)
Caudal-peduncle length	721-872(781)	784	97.0	826-965(881)
Soft-dorsal length in mm.	17.5-23.0(20.2)	20.0	....	11.0-17.5(12.9)
Thousandths of soft-dorsal length				
Distance from occiput to dorsal origin	400-469(434)	465	60.2	440-591(512)
Pectoral length	632-743(674)	840	14.4	780-982(868)
Snout length	195-232(205)	215	50.0	198-255(225)
Orbit length	175-211(195)	210	60.5	211-256(233)
Caudal-peduncle length	636-811(684)	725	19.9	808-982(860)
Head length	829-930(878)	925	52.0	874-1091(976)
AVERAGE HYBRID INDEX	....	....	57.5	....

*UGM—Union of gill membranes

different parental species. The squamation of the female hybrid differs from that of the male hybrid in that the cheeks and opercles are naked as they are in *E. spectabile* subsp. The cheeks and opercles of the male hybrid have embedded scales as in *E. r. cyanorum*. Embedded scales are found on the nape of both hybrids and also in both parental species. The breast of *spectabile*, but not usually *cyanorum*, is naked as are those of both hybrids.

The parental species also exhibit a striking difference in the infraorbital canal. In *spectabile* it is incomplete and has an average of 7.2 pores on each side of the head while in *cyanorum* it is complete with an average of 8 pores

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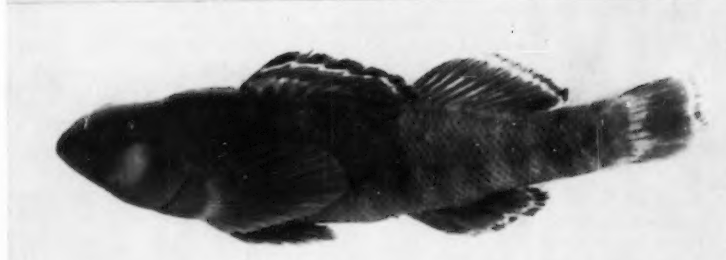

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Figs. 5-7.—5. *Etheostoma radiosum cyanorum*. Adult male (68.0 mm standard length) from Blue River 24 miles south of Ada, Oklahoma (from Moore and Rigney, 1952); 6. *Etheostoma* (*radiosum cyanorum* × *spectabile* subsp.). Adult male (61.0 mm standard length), locale as for fig. 5; 7. *Etheostoma spectabile* subsp. Adult male (54.5 mm standard length), locale as for fig. 5.

TABLE 5.—Comparison of the female hybrid, *Etheostoma* (*r. cyanorum* × *spectabile* subsp.), with female specimens of the parental species

Character	cyanorum Range (Average)	Hybrid Counts; Proportions	Hybrid Index	spectabile Range (Average)
Counts				
Pored lateral-line scales	46-53(49.3)	38	10.3	31-40(36.7)
Unpored lateral-line	4-10(7.1)	14	23.3	12-21(16.1)
Scales below lateral line	10-13(11.2)	8	5.8	7-9(7.8)
Scales around caudal peduncle	24-28(25.6)	23	35.0	19-24(21.6)
Proportions				
Standard length in mm.	51.5-59.8(54.0)	54.5	....	42.3-53.6(46.5)
Thousandths of standard length				
Snout length	60-71(67)	70	25.0	63-75(71)
Pelvic length	169-213(189)	206	34.6	194-239(215)
Premaxillary frenum width	24-31(28)	26	50.0	15-26(24)
Soft dorsal length in mm.	14.0-17.7(15.5)	16.5	....	11.4-14.8(12.5)
Thousandths of soft dorsal length				
Pelvic length	591-712(658)	678	81.8	712-860(813)
Distance from UGM* to pelvics	447-564(516)	582	35.2	568-661(618)
Caudal-peduncle length in mm.	11.6-13.7(12.4)	12.2	....	10.8-13.5(11.9)
Thousandths of caudal peduncle length				
Upper jaw length	354-416(379)	377	95.3	311-376(336)
Body depth	850-1034(952)	926	72.6	763-914(857)
Caudal peduncle depth	467-555(500)	467	53.5	391-469(429)
Body width	575-717(645)	623	61.4	526-683(588)
AVERAGE HYBRID INDEX	....	....	45.2	....

*UGM—Union of gill membranes

on each side. The infraorbital canals of the hybrids are incomplete thus indicating the influence of *spectabile*, but intermediate in that the two sexes average 7.5 pores on each side of the head.

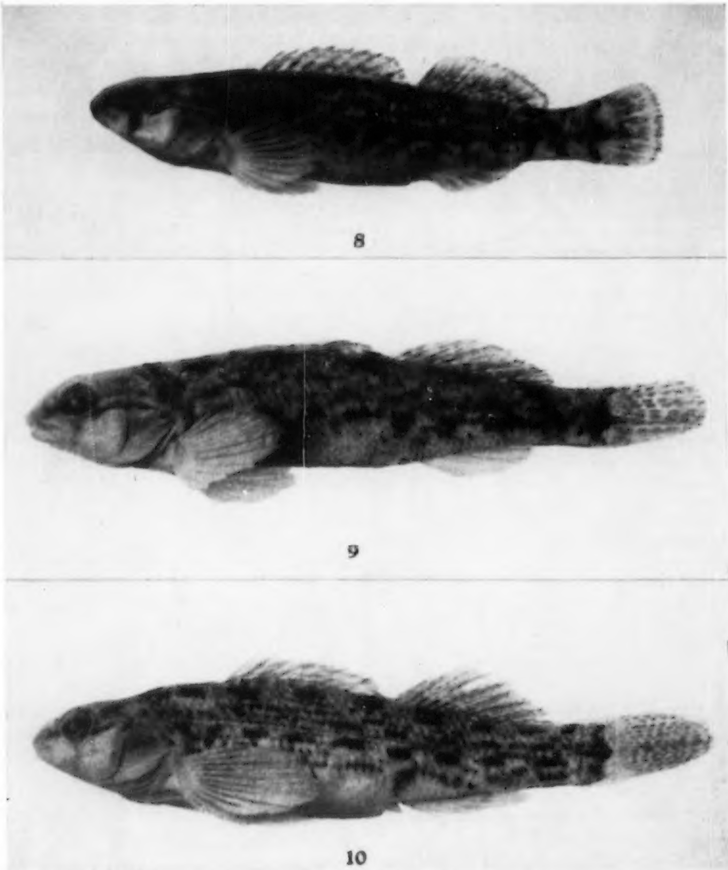
The color pattern of the male hybrid exhibits, for the most part, the direct influence of one or the other parent. The color description of the male is as follows: entire dorsum very dark with bars, alternating with olive-brown, extending diagonally downward and backward. Seven black bars extend around the body from the vent to the end of the caudal peduncle. The last three bars a greenish black with bright red interspaces.

Breast washed with green, opercles red and cheeks orange. A green bar extends downward from the eye and spreads out on the chin. Sides of belly washed with orange.

Spinous dorsal basally bright red and distally a bright green, the two colors being separated by a narrow white line. Soft dorsal basally red with a distal green bar, narrower than that of the spinous dorsal and separated from the red by a thin white line.

Caudal fin with two bright red basal spots, one above the other and, behind which, vertical bars of the following colors occur in order distally: brown, red (widest bar), light brown and green at the border.

Anal fin brilliant red with green border; pelvics green, with red and white in the swollen anterior fin-ray tips; and pectorals washed with orange and red.



Figs. 8-10.—8. *Etheostoma radiosum cyanorum*. Adult female (55.0 mm standard length), locale as for fig. 5 (from Moore and Rigney, 1952); 9. *Etheostoma* (*radiosum cyanorum* × *spectabile* subsp.). Adult female (54.5 mm standard length), locale as for fig. 5; 10. *Etheostoma spectabile* subsp. Adult female (53.6 mm standard length), locale as for fig. 5.

The influence of *E. r. cyanorum* is expressed by the dark head dorsum, bright caudal bars and basally red anal fin. On the other hand, the green breast, basal red on the dorsals and two basicaudal red spots reflect the influence of *E. spectabile* subsp. (figs. 5, 6 and 7; and table 3).

Most characters which show intermediacy in Table 4 do not indicate intermediacy in Table 5 and vice versa. This is probably due to the prominent sexual dimorphism expressed by the parental species in some of these characters. Therefore, an average of counts and measurements, taken from twenty specimens (ten males and ten females) of each parental species and the two

TABLE 6.—Comparison of the male and female hybrids, *Etheostoma* (*r. cyanorum* × *spectabile* subsp.), with male and female specimens of the parental species

Character	cyanorum Range (Average)	Hybrid Counts; Proportions	Hybrid Hybrid Index	spectabile Range (Average)
Counts				
Pored lateral-line scales	40-53(48.2)	40.5	26.5	31-41(37.5)
Unpored lateral-line scales	4-13(7.5)	12.5	57.4	12-21(15.2)
Scales above lateral line	7-9(8.0)	7.0	23.1	6-8(6.9)
Scales below lateral line	10-13(11.5)	9.0	30.6	6-9(7.9)
Scales around caudal peduncle	24-29(26.4)	24.0	51.0	19-24(21.5)
Proportions				
Standard length in mm.	51.5-66.4(57.3)	57.8	....	38.4-54.5(44.9)
Thousandths of standard length				
Caudal peduncle length	212-248(229)	231	92.8	239-278(257)
Pectoral length	197-254(227)	250	11.5	234-271(252)
Premaxillary frenum width	24-36(29)	26	25.0	15-31(25)
Distance from UGM* to pelvics	132-167(151)	162	21.4	155-178(165)
Head length in mm.	14.1-19.7(16.6)	16.9	....	11.5-15.8(13.2)
Thousandths of head length				
Distance from UGM* to pelvics	467-572(525)	573	11.1	508-629(579)
Soft dorsal length in mm.	14.0-23.0(17.9)	18.3	....	11.0-17.5(12.7)
Thousandths of soft dorsal length				
Distance from occiput to dorsal origin	400-562(475)	487	84.6	440-618(553)
Pectoral length	632-849(735)	790	67.1	780-982(902)
Pelvic length	522-712(629)	714	43.3	662-868(779)
Snout length	190-252(214)	223	72.3	198-273(247)
Body width	387-557(474)	488	72.5	430-588(525)
Distance from UGM* to pelvics	432-564(486)	531	55.9	483-661(588)
AVERAGE HYBRID INDEX	....	....	46.7	....

*UGM—Union of gill membranes

hybrids (one male and one female), so as to compute an average of each character and thereby obtain a value intermediate to the two sexes, were compared (table 6). In this comparison there are sixteen characters which give values between 0 and 100, with an average hybrid index value of 46.7.

Hubbs (1940), in his work with centrarchids, found that reciprocal crosses gave identical results. Therefore a comparison of male *spectabile* and female *cyanorum* with the two hybrids; and also the reciprocal cross, male *cyanorum* and female *spectabile*, was made.

Table 7 shows a comparison of ten female *cyanorum* and ten male *spectabile* with the two hybrids (one male and one female). Ten characters yielded index values between 0 and 100 with an average hybrid index value of 40.7.

Table 8 demonstrates the reciprocal cross using ten male *cyanorum* and ten female *spectabile*. In these data 26 characters yielded values between 0 and 100 with an average hybrid index value of 61.6.

Since the latter comparision yielded 16 more characters than the former, with values between 0 and 100, it might be concluded that the parents of the

TABLE 7.—Comparison of the male and female hybrids, *Etheostoma* (*r. cyanorum* × *spectabile* subsp.), with female specimens of *cyanorum* and male specimens of *spectabile*

Character	cyanorum Range (Average)	Hybrids Counts; Proportions	Hybrids Hybrid Index	spectabile Range (Average)
Counts				
Pored lateral-line scales	46-53(49.3)	40.5	20.0	35-41(38.3)
Unpored lateral-line scales	4-10(7.1)	12.5	25.0	12-16(14.3)
Scales above lateral line	7-9(8.0)	7.0	16.6	6-7(6.8)
Scales below lateral line	10-13(11.2)	9.0	33.3	6-9(7.9)
Scales around caudal peduncle	24-28(25.6)	24.0	62.8	19-23(21.3)
Proportions				
Standard length in mm.	51.5-59.8(54.0)	57.8	....	38.4-54.5(43.2)
Thousandths of standard length				
Caudal-peduncle length	217-243(230)	231	96.3	247-271(257)
Pectoral length	197-254(228)	250	29.0	234-271(259)
Distance from UGM* to pelvics	132-159(147)	162	25.0	157-175(167)
Soft dorsal length in mm.	14.0-17.7(15.5)	18.3	....	11.0-17.5(12.9)
Thousandths of soft dorsal length				
Pelvic length	591-712(658)	714	34.9	662-868(744)
Distance from UGM* to pelvics	447-564(516)	531	64.3	483-636(558)
AVERAGE HYBRID INDEX	....	....	40.7	....

*UGM—Union of gill membranes

hybrids were a male *cyanorum* and a female *spectabile* if, as Hubbs (1940) implied, systematic characters in fish hybrids tend to be intermediate between the parental species.

Although the tables are not included, comparisons were made as in tables 7 and 8 except that the hybrid sexes were treated separately. These comparisons yielded very much the same results as those obtained in tables 7 and 8.

Without experimental data it is apparently impossible to predict the appearance of the hybrids between the two possible reciprocal crosses, but if darter characters behave in the same manner as those of their relatives, the centrarchids, or as those of poeciliids (Hubbs, 1940), the data obtained in Table 7 and 8 should be closely similar. This is not true, since, as stated above, 16 more characters yielded values between 0 and 100 when male *cyanorum* and female *spectabile* were compared with the hybrids.

When we consider individual characters, there is sometimes a lack of expression in one sex suggesting the possibility that the character is of the sex-linked or sex-influenced type. For example, the so-called humeral scale is well developed in *E. r. cyanorum,* but poorly developed in E. *spectabile* subsp. The male hybrid resembles *cyanorum* in this character while the female does not. It seems possible, therefore, that in the cross between the two forms the emphasis of this character goes only to the male, whereas in ordinary matings it is or is not well expressed.

Squamation of the head is similarly expressed. The *cyanorum* head is quite regularly scaled and the *spectabile* head is naked. The hybrid male has scaley cheeks and opercles whereas the female has these areas naked.

It is evident that these percids present a somewhat different problem than

that of the centrarchids and poeciliids. Experimental work will be necessary to demonstrate the inheritance of some characters in *E. r. cyanorum* and *E. spectabile* subsp.

DISCUSSION

The Blue River System has a relatively rich fish fauna consisting of 49 known species which represent nine families and 32 genera.

TABLE 8.—Comparison of the male and female hybrids, *Etheostoma* (*r. cyanorum* × *spectabile* subsp.), with male specimens of *cyanorum* and female specimens of *spectabile*

Character	cyanorum Range (Average)	Hybrid Counts; Proportions	Hybrid Index	spectabile (Average) Range
Counts				
Pored lateral-line scales	40-51(47.1)	40.5	36.5	31-40(36.7)
Unpored lateral-line scales	4-13(7.9)	12.5	43.9	12-21(16.1)
Scales below lateral line	11-13(11.7)	9.0	30.8	7-9(7.8)
Scales around caudal peduncle	26-29(27.2)	24.0	42.9	19-24(21.6)
Proportions				
Standard length in mm.	52.5-66.4(60.5)	57.8	....	42.3-53.6(46.5)
Thousandths of standard length				
Orbit length	61-69(63)	67	50.0	67-76(71)
Caudal peduncle length	212-248(228)	231	89.3	239-278(256)
Soft dorsal length	306-354(333)	316	73.4	263-293(269)
Premaxillary frenum width	25-36(30)	26	33.3	15-26(24)
Head length in mm.	14.9-19.7(17.7)	16.9	....	12.4-15.8(13.7)
Thousandths of head length				
Orbit length	201-235(222)	228	68.4	228-252(241)
Caudal-peduncle length	721-872(781)	791	88.6	810-964(869)
Head depth	631-722(672)	638	34.6	591-664(620)
Soft dorsal length in mm.	17.5-23.0(20.2)	18.3	....	11.4-14.8(12.5)
Thousandths of soft dorsal length				
Distance from occiput to dorsal origin	400-469(434)	487	66.7	520-618(593)
Pectoral length	632-743(674)	790	55.6	797-974(935)
Pelvic length	522-649(599)	714	46.1	712-860(813)
Snout length	195-232(205)	223	57.1	236-273(268)
Upper jaw length	269-308(278)	295	63.8	284-342(325)
Caudal-peduncle length	636-811(684)	732	83.0	878-1022(967)
Orbit length	175-211(195)	211	77.9	243-274(268)
Body depth	632-755(693)	720	80.1	703-843(829)
Body width	387-486(431)	488	58.7	526-588(569)
Distance from UGM* to pelvics	432-498(455)	531	53.4	568-661(618)
Body depth in mm.	14.9-19.7(17.4)	13.2	....	9.2-11.7(10.2)
Thousandths of body depth				
Body width	574-674(619)	678	11.9	632-817(686)
Caudal-peduncle length in mm.	11.9-15.4(13.8)	13.4	....	10.8-13.5(11.9)
Thousandths of caudal peduncle length				
Upper-jaw length	377-429(406)	402	94.3	311-376(336)
Anal length	953-1326(1174)	1128	84.7	770-1031(874)
Body depth	867-1101(1014)	998	83.4	763-914(857)
Caudal-peduncle depth	487-601(558)	537	83.7	391-469(429)
AVERAGE HYBRID INDEX	....	....	61.6	....

*UGM—Union of gill membranes

The hybrid conbinations described in this paper probably originated by accident since there has been such a small number collected. The fact that there is interfertility between the parental species is indicative of their close relationship. Although the geographical ranges of the parents of each combination are superimposed, the species have maintained themselves as distinct species, indicating that interbreeding is not widespread. There has possibly been a breakdown of the complex isolating mechanisms which prohibit mass interbreeding by such distinct sympatric forms. (Blair, 1951).

The scarcity of recognized interspecific hybrids such as these has been discussed by Blair (1951), who suggested that isolating mechanisms are so effective that hybrids are rare. Blair also indicated that we do not appreciate the extent of hybridization in nature and may seldom recognize the hybrids which are produced, since so little work has been done.

Some of these barriers may have been broken down by the predominance of one parental species and an unbalanced sex ratio found in the parental species collected at Foraker. In a total of 175 specimens collected, 82.3% are *E. spectabile* subsp. and 61.2% of the total are females.

The sex ratios of the parental species collected from the Blue River are approximately 1-1, but there is a predominance of one parental species. In a total of 347 specimens collected from the same localities as the hybrids 62.5% are *E. r. cyanorum*.

A predominance of one species, accompanied by an unbalanced sex ratio, is an explanation proposed by Hubbs, Hubbs and Johnson (1943) for some catostomid hybrid combinations and also by Hubbs, Walker and Johnson (1943) for cyprinodonts.

A breakdown of ecological barriers may have altered the spawning habits of the species concerned. If one species spawns in the riffles and fast-moving water of the stream and the other in the pools directly below the riffles, it is quite possible that milt from the male riffle-spawner may be carried into the spawning beds of the other species in the pools and fertilize the eggs. This possible explanation is supported by field experience which indicates that *spectabile*, in Oklahoma, is most abundantly collected in quieter water and *cyanorum*, on the other hand, is taken, in breeding color, most often from riffles. This was proposed as a possible explanation for a cyprinid combination by Moore and Paden (1950).

Intensive studies of the breeding habits of the parental forms and the ecological conditions in the habitats will be necessary before definite conclusions can be drawn as to what combination of factors brought about hybridization.

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The Effects of Temperature and Moisture on the Reproductive Cycle of Scaphiopus h. holbrooki

Kenneth L. Gosner and Irving H. Black
Newark Museum, Newark, N. J.

Recent papers by Moore (summarized in Moore 1949) indicate the adaptive significance of embryonic thermal requirements in frogs of the northeastern United States. These requirements have significance in determining distributional limits, and breeding seasons appear to have become established in connection with them. Richmond (1947) and Ball (1936) both present data pertinent to a consideration of these requirements in northeastern *Scaphiopus h. holbrooki* but no detailed analysis of the problem has been published. The results of a field and laboratory investigation into this question are here presented.

In the northeastern United States the breeding activities of most species follow a seasonal pattern that is repeated with minor variations each spring. This type of behavior is contained in the concept of a mesic breeding behavior pattern (Bragg, 1945). In contrast, *S. h. holbrooki* illustrates the xeric breeding behavior pattern including the following points of interest: 1) Heavy rainfall is the primary control in the initiation of breeding activity; 2) In the usual sense there is no definite breeding season, reproductive activity is spasmodic and unpredictable; 3) Transient pools are resorted to even when more permanent situations are available; 4) Potentially, embryonic and larval development proceed at a very rapid rate.

Thus temperature and rainfall both play important parts in controlling the breeding cycle of tailless amphibians. In the northeastern United States temperature apparently has the more important role although the rainfall factor, from central New Jersey south in the coastal plain, may assume a more important role than it does farther north. This has been suggested by Noble and Noble (1923) who list *Bufo fowleri, Hyla andersoni* and *Scaphiopus holbrooki* as species whose reproductive activities are rain controlled. Volpe (1952) has shown a relationship between embryonic temperature requirements in *Bufo fowleri,* and the period utilized for reproductive activity. Both this species and *Hyla andersoni* appear to have their activities within the breeding season modified by the rainfall factor, but temperature still probably plays an important part in determining the beginning of the season. *S. h. holbrooki* shows still greater independence of environmental temperature and may breed concurrently with such early breeders as *Rana sylvatica* or with late breeders like *R. catesbeiana.* The question of the importance of temperature in the biology of *S. holbrooki* is therefore an interesting subject for closer inspection.

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MATERIALS

In April 1951 a breeding colony of *S. h. holbrooki* was discovered near Eatontown, Monmouth County, New Jersey. During 1951 and 1952 this colony was kept under close observation from March through June, visits being made approximately once a week and, during critical periods, almost daily. In addition to the Eatontown population this species has been observed by us in other parts of Monmouth, Ocean, Atlantic, Cape May, Cumberland, and Gloucester counties in central and southern New Jersey. As yet we have not taken *Scaphiopus* west of the Fall line in northern New Jersey although an American Museum of Natural History record lists it from Bergen County.

The breeding site at Eatontown is rather typical of those treated in the literature (Wright, 1932) and, so, will be described only briefly. Spring rains usually fill the lower end of an open goat pasture to a maximum surface area of about one quarter of an acre in very wet seasons. Unless constantly replenished by fresh rains the pool loses water rapidly, and is usually dry in summer. Permanently aquatic animals and plants are either absent entirely or very few in number.

This locality supplied eggs for a controlled study of larval growth rates and thermal requirements in 1951. Mated pairs from the same locality provided eggs for the study of embryonic growth rates and thermal requirements in 1952.

Climatic data have been obtained from the monthly meteorological summaries published for the Newark Airport station of the United States Weather Bureau (about 25 miles north of Eatontown). These records were compared with those from the Atlantic City and Trenton stations in an effort to approximate the probable conditions at the study site. Emergences that have come to our attention resulted in connection with major storms; the meterological data from the three stations agree sufficiently to warrant general estimates and this is the extent of the use made of this data. Occasional field observations of air and water temperatures supplement these data.

Eggs were secured from pairs mated in the laboratory. Larvae were secured, both from eggs collected in the field and from those laid in the laboratory. Stock groups and controls were kept in hard rubber photographic trays and in deep plastic refrigerator dishes at room temperature (18°-20°C). From the stock groups 10-15 eggs or larvae were taken for use in experiments, such groups being used only once and the survivors allowed to complete development in separate containers at room temperature. It was, thus, possible to consider the possibility of *delayed effects* evident up to the time of transformation. Cold experiments were made using water baths or a refrigerator, and warm experiments were carried out with water or sand baths heated by 25-40 watt electric lamps. In addition to periodic field collections, and observations, data were secured for rates of development at various air temperatures from groups reared in the museum garden and on the window sill of the museum.

TERMINOLOGY

The concepts employed in this problem are the *limiting temperatures* of Moore (1949), which we understand to represent the limits at which the embryonic and larval stages may reach a normal conclusion. The *upper* and

the *lower limiting temperatures* are, therefore, those at which the embryo is able to complete the stages resulting in the hatching of the egg and those at which the larva may develop to transformation. The *minimum* and *maximum* lethals are *absolute* tolerance limits and the result of exposure for short *periods* to temperatures beyond these limits is fatal. Between the lethals and the limiting temperatures, at both the cold and the warm ends of the scale, is a range of temperatures whose lethal effects are a function of the duration of exposure. We consider this range to be the one of more practical significance in this species under field conditions. At the lower tolerance limits rate of temperature change appears to have some importance. We found less individual variation and also a lower tolerance limit in tests when the temperature was lowered at a slow rate than when it was lowered rather rapidly. The rate of change did not appear very important in changes from lower to higher temperatures.

The concept of an *optimum* temperature for embryonic and larval development, is also used; it is defined as determining the highest obtainable rate of development resulting in the normal conclusion of a stage. This concept is consistent with other aspects of the breeding cycle of this form but is not necessarily appropriate for other animals.

The categories, *critical minimum* and *critical maximum* are employed only with reference to the larvae and have essentially the same meaning given to them by Cowles and Bogert (1944). These are temperatures inhibiting spontaneous activity to the extent that the animals are helpless. Complete narcosis occurs at levels somewhat beyond these limits. Since the limiting range is narrower than the critical range it is obvious that these represent lethals in the case of prolonged exposure.

EMERGENCE FOR BREEDING

Dates.—Breeding records for *S. h. holbrooki* are available from every month from March through August for the northeastern United States. Twenty-nine such records are summarized indicating the frequency of vocalizing or breeding choruses each month. For convenience all of our personal records for the same month and year are treated as single records: March 1, April 9, May 7, June 3, and August 5. Our earliest personal records for New Jersey are March 23, March 31 (eggs found in poor condition on both of these dates) and April 1, 1951 and 1952. This resumé is intended to indicate the extended period in which such activity may take place and does not represent an exhaustive analysis of the literature.

Factors controlling emergence.—Emergence for breeding purposes usually follows heavy rainfall. Several points complicate this picture: (1) Heavy rainfall does not always stimulate these animals to emerge even during the period when such appearances are to be anticipated. (2) There is considerable local variation in behavior between populations in the same general area and even between individuals of the same colony. During the very wet spring of 1952, e.g., colonies of *Scaphiopus* appeared in the Eatontown area and elsewhere in Monmouth County, New Jersey where investigation had failed to disclose any activity at previous times when the Eatontown colony was actively breeding. (3) Successional breeding may be of fairly frequent occurrence in this species. In 1951 the Eatontown colony bred on April 1 and again on May 23. On May 30, 1952 spadefoots were in chorus at Bennett, Cape May

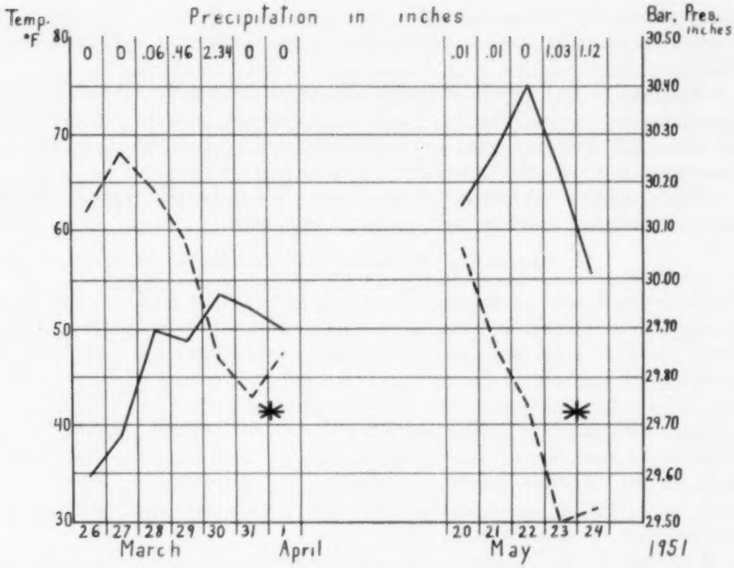

FIG. 1.—Summary of meteorological data for 2 breeding periods of *Scaphiopus h. holbrooki.* Daily average barometric pressure shown by broken line. Daily average temperature shown by solid line. Total daily precipitation shown at top of date columns. Ovulation occurred on dates marked by asterisks. Minimum pressure records are, March 29.53 on the 11th, April 29.36 on the 3rd, May 29.43 on the 23rd.

County, New Jersey, while young from an earlier breeding emergence were transforming at the same locality. Ball (1936) records a similar occurrence in Connecticut for *S. h. holbrooki.* Bragg and Smith (1942) record similar behavior for *Scaphiopus bombifrons* in Oklahoma. It has not been established whether females can breed more than once in a single season. It seems more likely that different individuals are involved.

Trowbridge and Trowbridge (1937) suggested that a minimum accumulation of moisture was required before the first spring emergence. Bragg and Smith (1942) emphasize the rate of fall rather than the amount. The minimum isolated fall that we associate with emergence for breeding is .82 in. Our observations indicate a considerable variation in the rainfall pattern preceding emergence. Thus the toads have appeared following a situation in which most (.63 in.) of a one inch fall came in two hour-long showers within a period of 4 hours. Strong choruses have also appeared following prolonged non-violent rains extending over several days.

We have observed delays in the appearance of a breeding chorus following minimum rainfall conditions ranging from 6 hours to 7 days. In the 7-day delayed emergence, a one-inch fall came over a three-day period (March 22-24, 1952) when surface temperatures were probably too low to permit emergence. No rain fell between March 24 and April 1 when a trace was recorded. At this time a large breeding chorus emerged at Eatontown in conjunction with a marked rise in surface temperature. Ball (1936) gives 7.5-8.6° C as threshold

temperatures for emergence. We have not observed the toads above the surface for breeding with air temperatures below a day long average of about 9.6° C.

Knepton (1951) published preliminary notes relating the release of active spermatozoa in *S. holbrooki* to changes in atmospheric pressure, but the results of this study have not yet been published in detail and the significance of pressure changes for the reproductive cycle is not yet clear.

Fig. 1 presents a summary of the changes in environmental conditions associated with two breeding emergences in this species.

EMBRYONIC THERMAL REQUIREMENTS

Lower limiting temperature.—Richmond (1947), as a result of field experience with this form in Virginia, estimates that water temperatures below 9.6°C produce some mortality, while temperatures below 4°C may result in almost 100% mortality. He records embryonic development taking place during a 7-day period in which the water temperature ranged from 4-14°C, the average being 6.5-11°C. The eggs may have been slightly warmer, having absorbed radiant heat—aided by black pigment and insulating membranes. Ball (1936) describes *Scaphiopus* breeding in Connecticut on April 16-18 with 'some hatching' on April 18. His thermal data show only minimum air temperatures ranging from 6-12°C.

On April 1, 1951 *Scaphiopus* ovulated at Eatontown, producing about 100 masses. An opportunity to visit the site did not occur until the following week, April 8, when no hatched larvae could be found and all of the masses had apparently disintegrated or decomposed. We have attempted, through an analysis of the meteorological reports for Newark and Atlantic City, to estimate the changes taking place at the pool during that week. Air temperatures dropped, from the average of 11.5-12°C on March 31-April 1 to an average of about 6.5°C on April 4, this period also being characterized by overcast skies. Air temperatures again began to rise on April 6 reaching an average of 11.5-14°C on this and the following day. On April 8 the water temperature at Eatontown was 9-10°C. Of the 72 hourly readings between April 3-5, 39 observations were of 7°C or less and of these 11 were of 4°C or lower.

It is our opinion that with these low nocturnal temperatures and in the absence of direct solar radiation because of overcast skies, the water temperature probably was driven down to 5-6°C where it remained probably for several days, thereafter rising to the 9-10°C mark. Hypothetical as this analysis is, our conclusions agree more or less with Richmond's estimates. The effect was 100% mortality under prolonged exposure to water temperatures of about 5-6°C. No *Scaphiopus* larvae were taken in the pool until after the May 23 ovulation. It may be noted that *Rana pipiens* eggs were found hatching a few miles from Eatontown on April 8 (lower limiting temperature according to Moore 5°C), thus indicating a tolerance for cold in this species greater than that of *Scaphiopus*.

In 1952 experiments were performed in an effort to ascertain the lower tolerance level with greater precision. Our experiments were performed with eggs laid in the laboratory by three pairs secured at the study locality.

A group of 75-100 eggs placed in a container, with a bath of cold running

water, hatched in 4 days at temperatures varying from 10-13°C (usually about 11°C).

A second group of about 30 eggs placed in a refrigerator in a covered plastic dish failed to hatch at a temperature of 5.5-6.5°C, the mortality being 100%. Almost no development beyond the early cleavage stages took place.

Our observations agree with those of Richmond (1947) in the matter of individual variation in thermal responses. It appears likely that we should place the lower limiting temperature (temperatures at which embryonic development may be completed), between 7 and 10°C, the higher temperature probably being closer to the average limit.

In an effort to secure data on the function of time with regard to the response to low temperature (duration of exposure vs. mortality), we placed a group of about 50 eggs in the refrigerator (5.5-6.5°C). Groups of 5 eggs each were removed periodically (twice daily) and efforts made to hatch them at room temperature. The eggs were in mid to late gastrula when placed in the refrigerator and no advance was observed during the experiment. All eggs removed during the first 72 hours hatched and the larvae eventually completed transformation. Of the eggs removed on the fourth day (115 hours) only about half hatched and continued to develop normally. Of the others removed on this day or on the two succeeding days, a few resumed development when returned to room temperature but the embryos became grossly deformed and died before hatching. By the 9th day all of the remaining embryos were obviously dead.

Possibly the most significant fact that emerges from these data is that the embryonic tolerance to cold in *Scaphiopus* is not equivalent to that of the other early breeders for which data are available (*Rana sylvatica* 2.5°C and *R. pipiens* 5°C *fide* Moore) and that any advantage the potentially high rate of development might give to the spadefoot is nullified by low temperatures of the order that may be expected from late March to mid-April.[1]

Upper Limiting Temperature.—Richmond (1947) offers evidence concerning the tolerance to high temperature by his mention of the completion of embryonic development at 33°C in 12 hours. We have found a high rate of mortality at this temperature, although some of our embryos also hatched in from 12 to 18 hours at 33°C. Approximately the same rate of development may be obtained at 29°C, however, and we suggest that temperatures above this are above optimum and the embryos are especially susceptible to the lethal effects of crowding. The upper limiting temperature is at about 29-33°C.

RATE OF EMBRYONIC DEVELOPMENT

Data have already been presented indicating the approximate rates of development at the tolerance limits. Thus, at the lower limiting temperature (7-10°C) approximately 168 hours are required, the rate increasing rapidly with an increase in temperature (about 100 hours at 12°C) to about 30-36 hours at 18-20°C and 12-18 hours at the upper limiting range of 29-32°C.

LARVAL THERMAL REQUIREMENTS.

Scaphiopus broods frequently fail as result of the disappearance of water.

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[1] *Hyla crucifer* and *Pseudacris feriarum,* both of which are also very early breeders, appear to be at least as tolerant to cold as is *Rana sylvatica.*

Thermal conditions in the medium in which larvae develop are, therefore, of considerable significance, as they affect the rate of growth. It has been mentioned that the rate of larval development is potentially very high. A characteristic of *Scaphiopus* larvae is the high rate of activity observed both in the field and in laboratory colonies.

Tests were run with larvae of the following size ranges: 10-12 mm, stage 23-25; 18-22 mm, leg buds just visible; and 24-28 mm, hind legs well developed or mature larvae nearing metamorphosis. Since no significant differences in response were found among these size groups, the data summarize the requirements for *S. h. holbrooki* larvae in general. It may be noted that responses vary individually and also according to the rate of temperature change, this being particularly true when the change is from higher to lower temperatures.

RESPONSES TO COLD

In one series of experiments the initial reduction in water temperature (19°C to 8.5°C) was carried out in about one and one-half hours with further reduction to 6°C accomplished in 8 hours, the final reduction to 2.5°C requiring 3 more hours.

Generally, normal activity is maintained with only slight inhibition at water temperatures of 10-11°C. Larvae become increasingly sluggish with further reduction in temperature but intermittent spontaneous activity remains down to 5-6°C. Most larvae become very sluggish at 8.5°C. No independent activity was observed at temperatures below 4.5°C and responses to tactile stimulus consisted of simple flexures. A few larvae responded very slightly to prolonged tactile disturbance even at 0.5°C.

The principal variations in response induced by slow or fast initial reductions in water temperatures involved recovery. In general a higher mortality rate was observed following a rapid lowering of the temperature, suggesting that *Scaphiopus* is able to modify its tolerances somewhat if the reduction in water temperature takes place slowly. Additional evidence on possible adaptation to cold is afforded by the observation that some cold adapted individuals recover normally from exposures of about 11 hours to a water temperature of 2.5°C while individuals transferred from 19°C directly to 2.5°C are killed immediately. Direct transfer to 6°C however, was not necessarily lethal, and direct transfer from cold to room temperature does not appear to effect recovery.

In an effort to determine the effects of prolonged exposure to cold, a group of larvae was subjected to a water temperature of 4-5°C for a period of several days. Roughly one-fourth of these larvae failed to survive exposure of about 16 hours, and less than one-quarter survived more than 40 hours.

From the above evidence we place the lower limiting larval temperature at about 10°C and the critical minimum at somewhat below 8.5°C. Survival at temperatures below this point is dependent upon duration of exposure. For some larvae, at least, the lethal minimum may lie but little above freezing.

The lower limiting temperature for larvae does not have the same significance it has for embryos. Some independent activity takes place at temperatures below this level and some larvae are able to survive more or less

prolonged exposure to still lower temperatures. However, we believe that this represents the threshold of developmental activity. At temperatures below this level normal activities are seriously curtailed and the larvae are held in a state of 'suspended animation.' For the embryos the lower limiting temperature is potentially a lethal limit since the suspension of the developmental processes for any prolonged period may result in a lethal disorganization of the various reactions involved. For larvae advanced to somewhat beyond stage 25 or thereabouts temporary suspension of development appears to be less critical.

RESPONSES OF LARVAE TO HEAT.

As in the previous experiments various larval stages were employed but no significant differences were observed.

Several conditions simplify the presentation of these data as compared with those for cold responses. First, there is less individual variation or, more properly, the range of individual variation is narrower. Second, differences in response depending on variations in the rate of change did not appear.

Water temperatures were raised from 18° to 37°C in about two and one-half hours. Locomotor activity increased somewhat at 23°C, and at 37°C nearly all larvae showed signs of discomfort. The advent of heat narcosis is indicated by a series of behavioral changes taking place rapidly between 37.5° and 38.5°C. The increased locomotor activity is at first interrupted by short quiescent intervals (normal *Scaphiopus* larvae are active almost continuously), and the appearance of rotational movements of a disorganized sort. These quiet intervals become increasingly long and locomotion more seriously disorganized until independent activity ceases entirely. Usually tactile stimuli will elicit some response but immediately prior to complete narcosis these responses take the form of simple flexures. A few larvae remain responsive at water temperatures slightly above 39°C, but in some the first signs of heat modified behavior occurred at 36.5°C.

The appearance of complete heat narcosis does not necessarily indicate a lethal exposure since some individuals remained in this condition for as long as 15 minutes at 38°-38.5°C and recovered when returned to room temperature. On the other hand exposures of 1 to 3 minutes at 38.5-39°C were lethal even though a few larvae remained responsive for periods up to 15 minutes during continued exposure at this level.

Recovery from 'sublethal' exposures required from 5 minutes to an hour or more. In several cases periodic 'relapses' to rotational or otherwise erratic behavior were noted during a period of several hours to several days following recovery even though these larvae eventually completed transformation. An additional note of interest was that even short exposures to unusually high temperature stimulated growth.

Reviewing these data, we place the lethal maximum at 38.5-39°C, the critical maximum at 37.5°C and the upper limiting larval temperature between 33° and 34°C. None of our larva survived continuous exposure at 34°C although some larvae completed transformation at 33°C. It may be noted, however, that mortality increases rather markedly at temperatures above 30°C and deleterious effects associated with crowding are accented when the water temperature reaches this level.

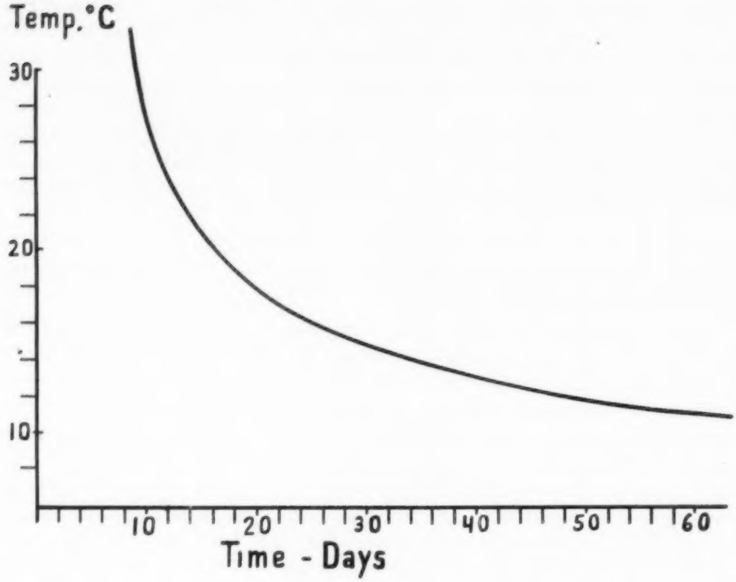

FIG. 2.—Approximate time-water temperature schedule for larval development in northeastern *Scaphiopus h. holbrooki.*

LARVAL GROWTH.

The curve of fig. 2 approximates the time-temperature schedule for normal development. Individual variations in growth rate in *Scaphiopus* are considerable and the 'runts' mentioned by Ball and others appeared in our groups, although cannibalistic tendencies did not. Even among normal individuals developing at optimum temperatures metamorphosis may take place during a period of several days to a week or more.

Wright and Wright (1949) give a range of 14 to 60 days as the time required for larval development. In our control groups, reared at room temperature (18°-20°C) larval development required 15 to 20 days although under crowded conditions the period was prolonged (30 to 36 days). At 28.5° to 33°C the required time was 9-10 days. The following is a summary relative to development at varying environmental temperatures. We placed a group of recently hatched *Scaphiopus* on the window sill of the museum on April 9; development was completed 52-56 days later. Driver (1936) reared groups at outdoor temperatures in Massachusetts starting April 24, transformations being completed 48 to 63 days later. Overton (1914) gives a two-month larval period for Long Island, New York starting in mid-April. Ball (1936) records a larval period of 23 days starting May 4 in Connecticut. At Eatontown the period was 17 to 20 days starting May 24. Abbott gives the larval period as 16 days in New Jersey in late June. Wright (1932) records a two-week period in late August.

DISTRIBUTIONAL CONSIDERATIONS

It appears likely that the center of origin of the genus *Scaphiopus* was near northern Mexico (Tanner 1939). The xeric breeding behavior pattern may have adaptive value particularly in this area (southwestern United States and northern Mexico) where supplies of surface water for breeding purposes may be available only after heavy rain. Variations in the time of occurrence and amount of such rain lead to further uncertainty as to when breeding situations will be available. Rapid loss of water is a characteristic feature of such habitats. Kincer (1922) describes an *Arizona rainfall type* for the probable ancestral region. In this type area heavy rainfall comes during July and August, usually. The *Plains rainfall type* also has its precipitation concentrated in the late spring and summer months. In the *Eastern rainfall type* area precipitation is more uniformly distributed. This means that in the northeast, stimulating rainfall sufficient to bring about the breeding emergence in *S. holbrooki* may be anticipated at almost any time during the rather extended period from March through August or September. It appears likely that the behavior of *S. holbrooki* is part of a behavior pattern common to the genus, this behavior having been retained by the *holbrooki* stock as it extended the range of the genus to the north and eastward.

The temperature tolerances of the embryological and larval stages in the spadefoot are more nearly equivalent to those of such late 'southern' breeders as *Rana catesbeiana* and *R. clamitans*. Although *Scaphiopus holbrooki* may breed concurrently with hardier 'northern' forms, like *Rana sylvatica* such behavior may be definitely disadvantageous. Temperature may, therefore, have fully as much significance for this form as it appears to have for the ranids, as a factor limiting northward distribution.

Scaphiopus h. holbrooki reaches the northeastern limits of its distribution in Massachusetts. For a species with such strongly developed burrowing habits edaphic conditions must also be of some importance and its occurrence in the northeast may be related to the occurrence of unconsolidated sediments. It occurs north of Georgia principally as a coastal plain and river valley species. Its secretive behavior gives a misleading impression of its relative abundance and spadefoots may be easily overlooked unless special efforts are made to detect them. Observations made during the very rainy spring of 1951 and 1952 apparently demonstrate that *S. h. holbrooki* is fairly generally distributed and, in fact, common on the New Jersey coastal plain.

SUMMARY AND CONCLUSIONS.

Breeding activity in *Scaphiopus h. holbrooki* is initiated by rainfall of approximately one inch or more, usually falling within a period of 24 to 48 hours. The pattern of precipitation varies from gentle steady rains to short violent downpours. Delays in the appearance of the spadefoots following rain vary from about 6 hours to as many as 7 days, emergence usually taking place at night; breeding activity normally lasts for two to three days. Temperature thresholds of 2.5°C for the upper soil layers and a 10°C or higher day-long average for the air at the surface have a controlling effect early in the season. Emergence in central New Jersey may be expected from about March 21 through August. In addition to the immediate rainfall stimulus a threshold accumulation of

moisture in the soil may be required to account for such variations in behavior within individual colonies as successional breeding, and also variations in the emergence of colonies subjected to similar 'short term' environmental stimuli. Readiness for emergence early in the season may also be influenced by the seasonal turnover in soil temperature.

Embryonic growth is limited by the ranges 7.5-10°C and 29-33°C, there being considerable individual variation in tolerance particularly at low temperatures. Below 10°C and above 29°C the rate of mortality increases noticeably. At minimum tolerable temperatures embryonic development may require as many as 7 days while at optimum temperatures, such development may be completed in 12 hours. 'Normal' development, requiring 36-48 hours, takes place at temperatures of about 16-21°C. At temperatures beyond the limiting levels the probability of survival varies with both the temperature and the duration of exposure.

Larval growth is limited by the thermal range 10-33.5°C approximately, there being considerable individual variation in responses particularly at low temperatures. Some larvae survive short exposure to water temperatures close to 0°C providing they have had time to become cold adapted. The maximum lethal is slightly above 38.5°C for most larvae. Critical limits are generally between 8.5° and 37.5°C. Larval growth at low temperatures requires up to about 60 days, while at optimum temperature (about 29°C) such growth may be completed in as few as 9 days. Northeastern broods beginning development in early April require about the maximum length of larval periods. Those hatching in early May (18-20°C water temperature) require up to about 30 days and June or July broods (25-27°) require about 16-20 days.

Without excluding or minimizing the possible importance of other factors, thermal requirements in this species appear to be fully as important as they are in *Rana* when considered as a factor determining the limits of distribution. The temperatures limiting embryonic development of *Scaphiopus holbrooki* are roughly equivalent to those of such 'southern species' as *R. clamitans* and *R. catesbeiana*. The range of tolerable temperatures may be somewhat wider in *Scaphiopus;* the two ranids breed in fairly large, thermally stable pools generally, while *Scaphiopus* chooses small transient pools that may be much less stable. The tolerances of *Scaphiopus* are not equivalent to those of such early breeders as *R. sylvatica* and *R. pipiens* and emergence with water temperatures below 16-20°C (before mid-May) may be definitely disadvantageous. Loss of water in the breeding pools is an important hazard to the successful completion of the breeding cycle. The high rate of development at higher temperatures may be regarded as an adaptation meeting this danger, but this advantage may be nullified by low temperatures.

Radiating from a center of distribution near northern Mexico, the subgeneric group, *Scaphiopus*, represented by *holbrooki* reached the eastern United States with a well developed xeric breeding behavior pattern. This pattern may have been an adaptation for the utilization of a rainfall peak coming in summer or late spring. *S. holbrooki* apparently has spread northward utilizing edaphically suitable territories; its distribution in the northeast (north of Georgia to the limit in Massachusetts) being principally that of a coastal plain and river valley species. Probably such territories include a fairly deep layer of uncon-

solidated sediments permitting the toads to burrow to sufficient depths to escape prolonged droughts and cold.

The ability of populations of this species to survive in the northeast may be due to the fact that in some years breeding activity does not begin until late spring or summer and to the fact that different parts of a colony may breed at different times.

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An Arrangement of the Subspecies of the Horned Toad, Phrynosoma Orbiculare (Iguanidae)

Samuel B. Horowitz
University of Chicago, Chicago, Illinois

The horned toads, *Phrynosoma orbiculare*, locally known as "camaléones" or "tapayaxin" are known to occur from northwestern Chihuahua and northeastern Sonora southward through the western mountains of Mexico to the southern end of the Mexican Plateau, and from the northern Sierra Madre Oriental of Nuevo León southward to Vera Cruz and the southern edge of the Central Plateau. The range may be stated as the southern central plateau and adjacent eastern and western mountains.

In this area the *camaléon* has become differentiated into five distinguishable subspecies.

The Mexican horned toad, type of the genus, was first mentioned in print by Hernandez (1651), 107 years before the 10th edition of the *Systema Naturae*. Despite this long history, there are relatively few synonyms for the name *orbiculare* assigned by Linnaeus. However, a brief historical review is essential to an understanding of the origin of some of the names used herein.

Historical Summary

Linnaeus' *Lacerta orbicularis* of the 10th edition of his *Systema Naturae* is indisputably the species under consideration. Linnaeus made reference to Hernandez (*loc. cit.*) who discussed and figured *P. orbiculare* in some detail. Wiegmann (1828) proposed the genus *Phrynosoma* to include *orbiculare*, *bufonium* (= *cornutum*) and *cornutum*.

Gray (1839) described *Phrynosoma wiegmanni* from a single specimen and six years later (1845) correctly listed the type specimen as *Phrynosoma orbiculare*. Duméril and Bocourt (1870, pl. 11) figured *Tapaya cortezii* and *T. dugesii*.[1]

Bocourt (1874) supplied the written description of *cortezii* and *dugesii* referring to the forms as *Tapaya orbicularis* var. *A* and *T. orbicularis* var. *B*

[1] Since the original description of *dugesii* from the Pacific slope of Colima no one has collected the form in the state nor has anyone claimed to have rediscovered it elsewhere. Mention of the subspecies has been made in the literature numerous times but only on the strength of Duméril and Bocourt's illustration and discussion.

The description given by Bocourt is not sufficiently explicit to allow the assignment of *dugesii* to any of the presently recognized subspecies. Furthermore, the Pacific slope of Colima is in a tropical biotic region whereas all other *P. orbiculare* are Nearctic in distribution. Thus it would be unwise to assign *dugesii* to its geographically closest neighbor *cortezii*.

Judgment on *dugesii* must await the examination of the types (probably in the Paris Museum) and a better knowledge of the fauna of the region in question. In the present paper no further reference will be made to *dugesii*: there is no trenchant reason, at present, either to perpetuate the name or to place it in synonymy.

respectively. The name *cortezii* is available for a subspecies recognized herein The last description of a new Mexican horned toad was that of Dugès (1888) who, described *T. o. longicaudatus* from the Valley of Mexico. For reasons presented later, both *P. wiegmanni* and *T. o. longicaudatus* are considered synonyms of the typical subspecies. Of the five subspecies recognized herein, only two have been named previously; therefore, three additional subspecies are described.

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PROCEDURE

The characters employed herein to distinguish the various subspecies of *Phrynosoma orbiculare* are used, for this purpose, in the present manner, for the first time. The choice of characters was preceded by a consideration of every readily mensurable feature (of which the author was cognizant) on the body of the horned toad. Those features which showed sufficient intrapopulation stability to make them potentially useful in the delineation of geographic variation were measured on all the individuals examined.

One hundred forty-two specimens of *P. orbiculare* with locality data have been examined. Of one form, *bradti*, only ten specimens have been available, while *durangoensis* is known from but eleven specimens. The subspecies best represented is *cortezii* with 44 specimens. The problems arising from this relative scarcity of material have been dealt with, in part, by the application of tests for statistical significance. These tests were applied when the value of a given character in separating two or more subspecies was in question. Furthermore, it has been the author's policy to include in the diagnoses of the subspecies only those differences that can be shown to be statistically significant. (Statistical significance is here defined as having a *P.* value of .05 or less in the tests used.)[3] In characters showing sexual dimorphism, tests for significance were applied to each sex. Both sexes of subspecies show all the differences found unless otherwise indicated. The same tests were used to detect sexual dimorphism.

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by $\mp$)[4] and the extremes are given for all characters found to be of value in differentiating the various subspecies.

The quantitative characters used herein to distinguish the various subspecies of *P. orbiculare* are as follows:

1. *Lateral fringe.*—The spines in the lateral fringe were counted on one side of the body, the right when possible. The count was made from the first enlarged spine above the insertion of the forelimb to the last enlarged spine in the lateral series, which is usually just above, or slightly anterior to, the insertion of the hindlimb. Females tend to have a slightly higher number of spines in the lateral fringe than males, but the difference is too slight and too variable to prove dimorphism in this character. Hence, as far as this character is concerned males and females are considered together.

2. *Ratio of head width to head length.*—This variable character, indicated in tabulations as HW/HL, is the best index to the relative body depression of the subspecies. *Phrynosoma* is a genus partly characterized by its flattened shape. The degree of depression in *P. orbiculare* will be shown to be one measure of specialization. Although measurements of body height and width would be valuable in calculating this depression, almost all of the material available had been in preservative for some time and the shape of the animals so altered that it was useless to measure these dimensions. In lieu of direct measurements on the body of the animal, measurements of the head, which maintained its original shape because of skeletal support, were used.

Head width was measured with the Vernier calipers held parallel to the transverse plane of the body, from the cheek region behind the angle of the jaws on one side, to the cheek region on the other side. This is not the widest dimension, which is dorsal and posterior to this point, on the temporal plateau.

Head length was measured with Vernier calipers from the tip of the snout to a point just behind the small projecting scale, the interoccipital of Smith (1946), between the two occipital horns.

There are differences between the sexes in the proportional width of the head, which is usually about three percent wider in females than in males. For this reason, the two sexes are considered separately.

The ratio of head width to head length is more variable among females than among males. Because of this the ratio can, in some cases, be shown to separate only the males of two races in question. In such cases the data for the females are not included in the diagnosis. They are, however, included in the summary of diagnostic characters.

3. *Femoral pores.*—The femoral pore counts given herein are the sum of the pores on the right and left femora and those in the preanal region. When, for any reason, the femoral pores could not be counted on one side of an animal, the count was disregarded. There is no significant difference between the sexes in the number of femoral pores in *P. orbiculare*, although on males the pores are often better defined and more distinct than on females.

4. *Ratio of tail length to body length.*—The ratio of tail length to body length will be indicated in tabulation as TL/BL. Body length was measured with Vernier calipers from the tip of the snout, along the ventral surface, to the vent. Tail length was measured with Vernier calipers from the vent, along the ventral surface of the tail to the tail's tip. Since *Phrynosoma* does not easily lose its tail, as do a number of iguanids, almost all the tails were intact. The tails of *P. orbiculare* average eleven percent longer in the male than in the female, so ratios are considered separately for each sex. Hereafter, tail length will be given as a ratio of body length and will be preceded by TL/BL.

5. *Ratio of occipital horn length to body length.*—The occipital horn is measured along its dorsal surface from the tip to the distal edge of the scales that surround the base. In taking this measurement, dividers and Vernier calipers are employed. No material sexual dimorphism is indicated in this character. Hereafter, the occipital horn length will be given as a ratio of body length and will be preceded by Occ/BL.

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[4] Klauber (1940) has been followed in using the standard error, rather than the probable error of the mean; the symbol ($\mp$) suggested by him has been used throughout.

Ontogenetic change.—The tail length proportion, the head width proportion and the occipital horn proportion are all subject to ontogenetic change. These changes are slight in the adult. In this study, therefore, only specimens over 50 mm in body length are utilized to calculate relative proportions. In this manner the error due to ontogenetic change is reduced to a practical minimum. Fifty millimeters represents the length above which gross variations from the mean for large animals are rare.

PHRYNOSOMA ORBICULARE (Linnaeus)

The body is greatly depressed, with the lateral fringes in single series. The spines of the lateral nuchal fringes are well developed. The head is not more than twenty-five percent wider than it is long. The ear is exposed. The nostrils are on or slightly above the poorly defined canthus rostralis. Only a single series of enlarged scales (the sublabials) is found between the infralabials. The distance between the infralabials and sublabials is never more than two or three scale rows wide. The infralabials are not coossified with the mandible. Two enlarged occipital horns are longer than the distance between their bases and are not continuous with the temporal series. Both temporal and occipital horn series lie in the frontal plane. The ventral scales are smooth. The tail is subterete, much longer than the head is wide and is more than forty percent of the body's length.

The head is narrower than long, as wide as long, slightly wider than long or wider than long. The supraocular crest is more or less depressed medially, and diverges posteriorly to form an acute or obtuse angle. The nostril is usually visible from above and faces laterally and forward; it may be on or slightly above the canthal ridge.

The temporal and occipital horns are invariably well-developed; their length always is greater than the distance between their bases. The two occipital horns may converge, point directly backward or diverge posteriorly. The scales surrounding the base of the occipital horn cover about one-third of the basal portion of the horn. The superciliary horn is distinctly enlarged.

The enlarged scales of the dorsal surface of the body are more or less regularly arranged in six columns and about five or six files, three columns on either side of the distinct median line. The columns converge posteriorly, the second and fourth rows continue along the dorsal surface of the tail, while the inner and outer rows are lost. The lateral fringe consists of a single series, the spines of which are more or less recurved.

Numerous series of modified scales are present on the head and neck region. The sublabials are usually 10 or 11 but may vary from 8 to 13 and are rarely the same on each side; the infralabials are usually 11, 12 or 13, rarely 10 or 14; the supralabials are usually 7, 8 or 9, rarely 6, 10 or 11. The scales of the labial series enlarge posteriorly. The last few scales of the sublabial series, however, show a decline in size. A series of three or four auricular lobules is terminated below by a postrictal, which is occasionally paired. Behind the ear is a nuchal dermal fold bordered by about six spines which increase in size posteriorly. The tympanum is visible. A row of about five spines subtends the anterior portion of the nuchal dermal fold.

The ventral scales are pointed (rarely notched) and directed posteriorly and laterally with the exception of the median gular scales, which are directed

posteriorly. The femoral pores may be located almost anywhere on their containing scale and may or may not engage the edge of the scale. The femoral series extend onto the postanal or interfemoral area, and sometimes occur in three rows in that region. The scales bearing the femoral pores are smooth and may or may not be notched behind.

The pattern consists of paired dark nuchal blotches followed by spots of varying size that may show some consistency at the subspecific level. The spots are usually close to the median line and are sometimes edged behind, and more rarely in front, by light borders.

PHRYNOSOMA ORBICULARE ORBICULARE (Linnaeus)

Lacerta orbicularis Linnaeus, 1758, Systema Naturae, ed. 10:365. Mexico City. By restriction (Smith and Taylor, 1950:329).

Phrynosoma wiegmanni Gray, 1839, *in* Zool. Beechey's Voyage:96. Mexico City. By restriction (Smith and Taylor, 1950:329).

P. orbiculare Gray, 1845, Cat. Spec. Lizards Coll. British Mus. (see P. wiegmanni, *supra.*):228; Boulenger, 1885, (in part), Cat. Lizards British Mus., ed. 2, 2:242; Cope, 1887, (in part), U.S. Natl. Mus. Bull. 32:38-39; Garman, 1887, (in part), Bull. Essex Inst. 19:12; Cope, 1900, (in part), Rept. U.S. Natl. Mus. 1898:417-419; Terron, 1932, (in part), An. Inst. Biol. Mexico 3(2):104-108; Smith and Laufe, 1945, (in part), Trans. Kansas Acad. Sci. 48(3):336-338.

Tapaya orbicularis Girard, 1858, U.S. Expl. Exped. (Wilkes) 20:394. Valley of Mexico. Duméril and Bocourt, 1870, 1874, (in part), Miss. Sci. Mexique et l'Amerique Centrale 3, sec. 1:221-222, pl. 11, fig. 1, a-g; Rovirosa, 1888, La Naturaleza, Ser. 2. 1(4):156; Herrera, 1890, La Naturaleza, Ser. 2.1:332; Dugès, 1896, La Naturaleza, Ser. 2. 2(11):479.

Tapaya orbicularis longicaudatus Dugès, 1888, La Naturaleza, Ser. 2. 1(3):117. Valley of Mexico.

Phrynosoma o. orbicularis Günther, 1902, (in part), Biol. Centrali-Americana (Reptilia and Batrachia):78. Mexico City.

P. orbicularia Ruthling, 1919, Copeia (72):68. Valley of Mexico.

P. o. orbiculare Smith, 1934, Trans. Kansas Acad. Sci. 37:290, pls. 11 and 12, figs. 2 and 5. Between Mexico City and Cuernavaca. Smith and Necker, 1943, An. Escuela Nac. Cien. Biol. 3:216-218; Smith and Taylor, 1950, Univ. Kansas Sci. Bull. 33, pt. 2(8):329; 1950, U.S. Natl. Mus. Bull. 199:97; Reeve, 1952, (in part), Univ. Kansas Sci. Bull. 34, pt. 2, (14):936-940.

Diagnosis.—The typical subspecies differs from *orientale* and *cortezii* in having fewer lateral spines, (m. 22.9 $\mp$ 0.4, 19-28), and in the narrower head of the male (HW/HL m. 1.03 $\mp$ 0.02, 0.97-1.08 (1.16)). *P. o. orbiculare* further differ from *orientale* in having more femoral pores (m. 31.5 $\mp$ 0.7, 24-39). It differs from *bradti* and *durangoensis* in having fewer femoral pores and a proportionately shorter tail (TL/BL male m. 0.66 $\mp$ 0.01, 0.60-0.75; female m. 0.56 $\mp$ 0.01, 0.52-0.58). It also differs from *bradti* in having proportionately longer occipital horns (Occ/BL. m. 0.060 $\mp$ 0.002, 0.050-0.073).

Size.—The largest specimen, a female, is 83 mm in body length; the largest male is 78 mm in body length.

Range.—The state of Mexico and at least northern Morelos. The distribution of this subspecies approximates Moore's (1945, pp. 217-236) Aztec faunal district of the Transverse Biotic Province. The range of the form does not include southern Hidalgo and northern Puebla as does the Aztec faunal district.

Material examined.—Thirty-six specimens of the subspecies from 14 localities were examined, as follows: MEXICO AND THE FEDERAL DISTRICT: Lerma, 1 (EHT No. 23989); Mexico City, 5 (USNM Nos. 12717, 47043-47046); near Mexico City, 4 (MCZ No. 4529 plus 3 specimens); Valley of Mexico, 6 (USNM No. 194 plus 5 specimens); 11 miles south of Mexico City, 1 (EHT 23981); Rio San Buenaventura

at Tlalpan, 1 (CNHM No. 17113); Rio San Juan de Díos at Distrito Federal, 1 (CNHM No. 17112); between Nativitas and Chalco, 1 (EHT No. 19233); 1 mile west of San Barolito, 3 (AMNH Nos. 15426-15428); East of Santa Cruz, 1 (AMNH No. 18482); San Juan Teotihuacan, 4 (MCZ Nos. 6346, 16056, USNM No. 19016, CNHM No. 48532); 3 miles west of Tacula, 3 (AMNH Nos. 15423-15425); Toluca Valley, 2 (USNM Nos. 47360-47361); Tlalnepaubla (Tlalnepautla), 3 (CNHM Nos. 17114-17116).

Discussion.—The type locality of *orbiculare* has never been ascertained, nor can it be inferred from the data given by Linnaeus. Linnaeus' reference to the description by Hernandez (1651) is of little value. Hernandez mentions specimens from "New Spain," an area that encompasses most of present day Mexico. Smith and Taylor (1950) arbitrarily restrict the type locality of *orbiculare* to Mexico City. This solution is acceptable to the author, as it is not unlikely that the original Hernandez specimens came from this area.

Through the courtesy of Mr. J. C. Battersby of the British Museum, pertinent data on *P. wiegmanni* Gray are available. The type specimen is a dry skin stuffed with sawdust, so no reliable measurements are possible. However, the data available are sufficient to indicate that *wiegmanni* is a synonym of *orbiculare*. Battersby (*in litt.*) gives the femoral pore count as approximately 37 (the dried condition precludes an exact count), the lateral fringe count as 24, and says that the occipital horns project slightly further backwards than do the temporal horns. This combination of characters restricts allocation of *wiegmanni* to *durangoensis* or *orbiculare*. The undeveloped nature of the country in which *durangoensis* occurs, the relative inaccessibility, even today, of the southern Sierra Madre Occidental, the home of *durangoensis*, makes it extremely unlikely that the type of *wiegmanni* is *durangoensis*. Pending evidence to the contrary, the restriction of the type locality of *P. wiegmanni* to Mexico City, by Smith and Taylor (1950) is acceptable and *P. wiegmanni* is assumed to be a synonym of *P. o. orbiculare*.

Smith and Necker (1943) correctly consider *Tapaya orbicularis longicaudatus* of Dugès (1888) from the Valley of Mexico to be a synonym of *orbiculare*. The locality, description and photographs of the type leaves no question concerning its identity.

Phrynosoma orbiculare bradti n. subsp.

P. orbiculare Dunn, 1936, (in part), Proc. Acad. Nat. Sci. Philadelphia 88:475. 21 miles south of Miñaca, Chihuahua.

P. o. orbiculare Taylor and Knobloch, 1940, Proc. Biol. Soc. Washington 53(26):125. Mojarachic, Chihuahua. Smith and Taylor, 1950, (in part), U.S. Natl. Mus. Bull. 199:97; Reeve, 1952, (in part), Univ. Kansas Sci. Bull. 34, pt. 2 (14):936-940.

Diagnosis.—This subspecies, although closely related to *durangoensis*, differs from that subspecies and all of the other races of *P. orbiculare* in possessing a remarkably high number of femoral pores (m. 49.0 ∓ 1.3, 43-55). The present subspecies differs from all other subspecies, except *durangoensis*, in having a proportionately longer tail (TL/BL male m. 0.72 ∓ 0.01, 0.71-0.73; female m. 0.62 ∓ 0.02, 0.59-0.65). The males of *bradti* have a proportionately shorter tail than the males of *durangoensis*. Furthermore, *bradti* differs from *cortezii* and *orientale* in having fewer spines in the lateral fringe (m. 23.3 ∓ 0.5, 21-26). The males of *bradti* have proportionately narrower heads than the males of *cortezii* and *orientale*. The females of *bradti* are narrower headed than the females in *orientale* (HW/HL male m. 1.01 ∓ 0.01, 0.98-

1.03; female m. 1.04 ∓ 0.02, 1.00-1.07). *P. o. bradti* differs from *orientale* and *orbiculare* in its proportionately shorter occipital horn length (Occ/BL m. 0.050 ∓ 0.002, 0.045-0.057).

Type.—No. 68962, a young female, in the collection of The American Museum of Natural History, collected by George M. Bradt, on May 2, 1948 at Caborachic, Chihuahua, Mexico. The location of Caborachic is given by the collector as 15 miles south of Guachochic, Chihuahua, at an altitude of 8000 feet.

Description of the type.—The head is slightly wider than long; its dorsal profile curves smoothly from the snout to the tip of the occipital horns, the curvature being more acute anteriorly. The supraocular crest is depressed medially, and diverges posteriorly to form an obtuse angle. The nostril is visible from above, facing laterally forward, on, but mostly above, the poorly defined canthal ridge.

The temporal and occipital horns are well-developed, but short. The occipital horns are about three times as long as the distance between their bases, and project beyond the temporal horns.

The continuity of the right lateral fringe is broken once anteriorly. The spines of the fringe are about one and one-third as high as wide, and are slightly recurved. There are 23 spines in the lateral fringe.

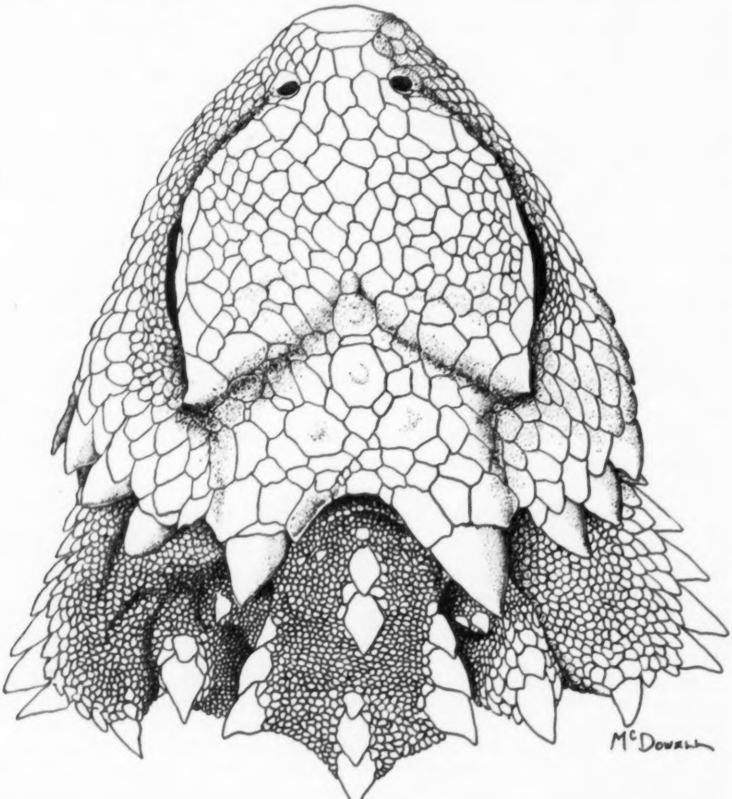

Fig. 1.—A dorsal view of the head of *Phrynosoma orbiculare bradti*. The specimen is a young male, AMNH No. 68963, a topotype, from Caborachic, Chihuahua. The asymmetry of the occipital horns is an atypical condition.

The femoral pores number 55. They occur in three rows in the preanal region reducing to two and then to one row as the pore series reaches the femur. Each femoral pore is located well back from the edge of the scale. Some of the femoral scales are notched behind.

The type has a snout to vent length of 57 mm; the tail length is 37 mm, or 65 percent of the body length. The hind leg is 39 mm long; comprising 68 percent of the body length. The head width at the angle of the mouth is 15.8 mm; the head length is 14.7 mm; the head width is 107 percent of head length; the supraorbital crest is 9.4 mm wide; the supraorbital crest width is 64 percent of the head length, and 60 percent of the head width.

The dorsal surface of the head and body of the type is a uniform slate grey except for a light area at the base of the occipital horns. The base of the tail is also slate grey but the distal portion is lighter with distinct dark crossbars, which are narrower than the lighter interspaces.

Ventrally the type (in alcohol) is dirty white, irregularly mottled with black and rather heavily mottled in the pectoral, gular and chin regions. The underside of the tail is dirty white, with only a vestige of the black bars that cross the dorsal surface.

Size.—The largest specimen, a female, has a body length of 81 mm. The largest male measures 78 mm from snout to vent.

Range.—Known from the northern Sierra Madre Occidental in Chihuahua and almost certainly Sonora.

Material examined.—The subspecies is based on 10 specimens including the type, from 7 localities as follows: CHIHUAHUA: East of Babicora, 1 (AMNH No. 68313); 30 miles west of Balleza, 1 (AMNH No. 68961); Caborachic, 2 (AMNH Nos. 68962-68963); 21 miles south of Miñaca, 1 (ANSP No. 20001); Mojarachic, 1 (EHT No. 23046); Samachique, 3 (CNHM Nos. 11826, 15725-15726). SONORA: "North Sonora," 1 (AMNH No. 538).

Phrynosoma orbiculare durangoensis n. subsp.

P. orbiculare Boulenger, 1885, (in part), Cat. Lizards British Mus., ed. 2. 2:241. Ciudad, Durango.

P. o. orbicularis Günther, 1902, (in part), Biol. Centrali-Americana (Reptilia and Batrachia):78. Ciudad, Durango.

P. o. orbiculare Smith, 1939, Ann. Carnegie Mus. 27, art. 21:315. Coyotes, Durango. Smith and Taylor, 1950, (in part), U.S. Natl. Mus. Bull. 199:97-98; Reeve, 1952, (in part), Univ. Kansas Sci. Bull. 34, pt. 2 (14):936-940.

Diagnosis.—A subspecies of *P. orbiculare* closely related to *bradti*, from which it differs in having fewer femoral pores (m. 41.7 ∓ 1.6, 35-46 (51)) and in having a proportionately longer tail in males. *P. o. durangoensis* differs from *cortezii* and *orientale* in having a proportionately narrower head (HW/HL male m. 0.98 ∓ 0.03, 0.95-1.01; female m. 1.04 ∓ 0.01, 1.01-1.06) and in having fewer spines in the lateral fringe (m. 22.8 ∓ 0.6, 20-26). It differs from the latter two subspecies and *orbiculare* in having a proportionately longer tail length (TL/BL male m. 0.79 ∓ 0.01, 0.78-0.79; female m. 0.63 ∓ 0.03, 0.57-0.70).

Type.—No. 68359, an adult female in the collection of The American Museum of Natural History, was collected by the David Rockefeller Mexican Expedition, on August 8, 1947, 10 miles east of El Salto, District of Durango, Durango, Mexico, at an altitude of about 8000 feet.

Description of the type.—The head is slightly wider than long, its dorsal profile curves more or less smoothly from the snout to a point at the posterior margin of the supraocular crest, with the curvature more acute anteriorly. The supraorbital crest is slightly depressed medially, diverging posteriorly to form an obtuse angle. The nostrils are visible from above and face laterally and forward on the rounded canthal ridge.

The temporal and occipital horns are well-developed though short. The occipital horns project behind the temporal horns. The occipital horns are about three times as long as the distance between their bases.

The right postrictal of the type is damaged. The lateral fringe is continuous. The

spines of the lateral fringe are about one and one-third as long as wide, are recurved and there are 21 on the right side. There are 42 femoral pores.

The type has a snout to vent length of 85 mm; the tail length is 52 mm; the ratio of tail length to body length is 61 percent. The hind leg is 52 mm long, 61 percent of the body length. The head width at the angle of the jaws is 20.5 mm; the head length is 19.4 mm; the head width is 106 percent of the head length; the supraorbital crest is 11.6 mm wide; the supraorbital crest width is 62 percent of the head length, and 57 percent of the head width.

The general body color is light slate grey; the head is lighter grey with diffuse blue and light pink areas. Two black nuchal spots are present and are flanked anteriorly by light slate blue on the upper surfaces of the dermal fold.

Ventrally the type is mottled black. Incomplete black bands traverse the underside of the tail.

Size.—The largest specimen, a male, has a body length of 90 mm. The largest female has a body length of 85 mm.

Range.—The Sierra Madre Occidental of Durango, Jalisco and Zacatecas.

Material examined.—The subspecies is based on 11 specimens including the type, from 5 localities, as follows: DURANGO: Coyotes, 6 (CNHM Nos. 1505 plus 1 specimen, 1507 plus 3 specimens); El Salto, 1 (USNM No. 47469); 10 miles east of El Salto, 2 (AMNH Nos. 68358-68359). JALISCO: near Bolaños, 1 (USNM No. 47872). ZACATECAS: Sierra Madre, 1 (USNM No. 47873).

PHRYNOSOMA ORBICULARE CORTEZII (Duméril and Bocourt)

P. orbiculare Duméril and Bibron, 1837, (in part), Erpetologie Géneral 4:321-323. Vera Cruz. Duméril and Duméril, 1841, Cat. Meth. Coll. Reptiles Paris:78; Sumichrast, 1882, (in part), La Naturaleza 6:38; Perez, 1886, Proc. U.S. Natl. Mus. 9:194; Cope, 1887, (in part), U.S. Natl. Mus. Bull. 32:38-39; Mocquard, 1899, Bull. Soc. Philom., ser. 9, 1:156; Cope, 1900, (in part), Rept. U.S. Natl. Mus. 1898:417-419; Terron, 1932, (in part), An. Inst. Biol. Mexico, 3 (2):104-108, fig. 6; Smith and Laufe, 1945, (in part), Trans. Kansas Acad. Sci. 48(3):336-338.

Tapaya Cortezii Duméril and Bocourt, 1870, Miss. Sci. Mexique et l'Amérique Centrale 3(1) pl. 11, fig. 2, a-g. See *T. orbicularis* var. *A*.

T. orbiculare Bocourt, 1874, (in part), Miss. Sci. Mexique et l'Amérique Centrale 3(1):221-222. Vera Cruz.

T. orbicularis var. A Bocourt, 1874, *ibid.*:223-224. Hacienda del Jasmin, between Orizaba and Cordova, Vera Cruz.

Phrynosoma orbicularis Barcena, 1874, (in part), La Naturaleza, Ser. 1. 3:45-47. Jalisco.

P. orbiculare cortezii Boulenger, 1885, Cat. Lizards British Mus., ed. 2. 2:242. Jalapa and Orizaba, Vera Cruz and Puebla, Puebla. Blatchley, 1893, Proc. U.S. Natl. Mus. 16(922):41; Günther, 1902, Biol. Centrali-Americana (Reptilia and Batrachia):78; Smith, 1934, Trans. Kansas Acad. Sci. 37:291, pls. 11 and 12, figs. 1 and 6; 1939, Field Mus. Nat. Hist. 24(4):23; Smith and Taylor, 1950, Univ. Kansas Sci. Bull. 33, pt. 2 (8):349; 1950, U.S. Natl. Mus. Bull. 199:98; Reeve, 1952, Univ. Kansas Sci. Bull. 34, pt. 2 (14):933-935.

Tapaya orbicularis Dugès, 1888, (in part), La Naturaleza, Ser. 2. 1(3):116-117. Guadalajara. 1896, La Naturaleza, Ser. 2. 2(11):479.

Phrynosoma orbiculare orbicularis Günther, 1902, (in part), Biol. Centrali-Americana (Reptilia and Batrachia):78. North of Rio Santiago, Jalisco.

P. douglassii ornatissimum Cope, 1900, (in part, not of Girard, 1858), Rept. U.S. Natl. Mus. 1898:417. Jalapa, Vera Cruz.

P. o. orbiculare Del Campo, 1936, An. Inst. Biol. Mexico 7:275. Actopan, Hidalgo. 1937, An. Inst. Biol. Mexico 8(1 and 2):263; Reeve, 1952, (in part), Univ. Kansas Sci. Bull. 34, pt. 2(14):936-940.

Diagnosis.—This, the closest related subspecies to *orientale*, differs from that form in possessing more femoral pores (m. 32.3 ∓ 0.6, 24-42. The present subspecies differs from *orbiculare*, *bradti* and *durangoensis* in possessing a greater number of spines in

the lateral fringe (m. 28.0 ∓ 0.3, 24-32). The males of *cortezii* differ from the males of *orbiculare*, *bradti* and *durangoensis* in having a comparatively wider head (HW/HL male m. 1.10 ∓ 0.02, 1.02-1.19). *P. o. cortezii* may also be distinguished from *bradti* and *durangoensis* by its proportionately shorter tail (TL/BL male m. 0.62 ∓ 0.02, 0.51-0.68; female m. 0.53 ∓ 0.01, 0.43-0.60).

Size.—The largest specimen, a female, has a body length of 93 mm. The largest male has a body length of 86 mm.

Range.—Southern Zacatecas, exclusive of the mountains, Jalisco, exclusive of the mountains, east to eastern Hidalgo south through western Vera Cruz to central Puebla. The major portion of the range is in the Transverse Volcanic Biotic Province of Moore (1945). *P. o. cortezii* also is found in the extreme southern part of the Chihuahua-Zacatecas Biotic Province of Goldman and Moore (1946).

Intergradation takes place with *orientale* in the southwestern part of the state of San Luis Potosi.

Material examined.—Forty-four specimens of the subspecies from twenty localities were examined, as follows: HIDALGO: El Chico National Park, 1 (EHT No. 19718); between El Durazno and Cornacustla, on the Pan American Highway, 1 (AMNH No. 62322); Guerrero Mill, below Real del Monte, 4 (MCZ Nos. 11311, 11313 and 11315-11316); Hacienda de Velasco, near Omitlán, 1 (MCZ No. 17086); between Tizayuca and the road to Tolcayuca, 1 (AMNH No. 62319); near Tulacingo, 1 (EHT No. 19236); 270 kilometers north of Mexico City, 1 (CNHM No. 37017). JALISCO: Guadalajara, 1 (AMNH No. 537). PUEBLA: Chalchicomula, 3 (MCZ Nos. 14095-14097); Puebla, 1 (MCZ No. 9556); San Diego, 3 (USNM Nos. 111365-111367); San Martin, 1 (USNM No. 47706). VERA CRUZ: 1 (ANSP No. 12832); Encino Gacho, 1 (AMNH No. 62321); Jalapa, 4 (MCZ No. 2851 and USNM No. 4596 plus 2 specimens); 15 miles east of San Marios, 5 miles west of Perote, 1 (EHT No. 10446); Las Vigas, 7 (USNM Nos. 47318-47324). ZACATECAS: 27 miles north-west of Fresnillo, 1 (UI No. 6727); Plateado, 10 (USNM Nos. 47874-47882, 47927).

Discussion.—The only locality mentioned in the type description of *cortezii* is "Hacienda del Jasmin, between Orisaba (sic) and Cordaba (sic), Vera Cruz." This, then, is the type locality.

P. o. cortezii, a widespread and variable form, may be divisible into two or more subspecies. The specimens from the eastern part of the range, from the states of Vera Cruz and Puebla, average proportionately longer tails than those of the west. If, when additional specimens are available, this difference proves constant the western populations will require a new name.

PHRYNOSOMA ORBICULARE CORTEZII-ORIENTALE intergrades

P. orbiculare Garman, 1887, (in part), Bull. Essex Inst. 19:12. San Luis Potosi.

P. o. orbiculare Smith and Taylor, 1950, (in part), U.S. Natl. Mus. Bull. 199:98. Jesús María, San Luis Potosi; Reeve, 1952, Univ. Kansas Sci. Bull. 34, pt. 2 (14):936-940.

Thirteen specimens from southwestern San Luis Potosi are considered intergrades between *cortezii* and *orientale*. The mean femoral pore count (m. 27.3 ∓ 1.7) of these populations is halfway between that of the two subspecies. The observed range of femoral pores is 16-33, this overlaps most of the range of both subspecies. The lateral fringe number (m. 30.5 ∓ 0.7) of the intergrades is between that of *cortezii* and *orientale*. The tail to body ratio of the male (TL/BL m. 0.59 ∓ 0.04) is unexplainably, although not significantly, lower than that of either *cortezii* or *orientale*. The tail to body ratio of the female (TL/BL m. 0.52 ∓ 0.03) is slightly lower than that of either *cortezii* or *orientale*.

On the basis of femoral pore counts, some of the specimens from the localities in what appears to be a region of intergradation can be assigned to one or the other of the subspecies. However, when the means are considered, assignment to either subspecies is impossible for all localities, with a single exception. A specimen from Sapotillo (a district of Guadalcázar), is assignable to *cortezii*. This specimen, closest to the known range of *orientale*, is also considered an intergrade on these grounds.

Material examined.—The intergrade specimens come from the following localities: SAN LUIS POTOSI: Jesús María, near the mountains, 3 (USNM Nos. 47157-47159); near San Luis Potosi, 5 (MCZ Nos. 19065 and 4549 plus 3 specimens); 9 miles southwest of San Luis Potosi, 2 (EHT Nos. 23954-23955); Sapotillo, 1 (AMNH No. 69702); Sierra de San Miguelito, 9 leagues south of San Luis Potosi, 2 (MCZ Nos. 4531 and 4536).

Phrynosoma orbiculare orientale n. subsp.

P. orbiculare Garman, 1887, (in part), Bull. Essex Inst. 19:12. Sutherland Springs, Texas. Dunn, 1936, (in part), Proc. Acad. Nat. Sci. Philadelphia 88:475.

P. o. orbiculare Smith and Taylor, 1950, (in part), U.S. Natl. Mus. Bull. 199:98. San Pedro, San Luis Potosi; Hacienda Pablillo, Nuevo León. Reeve, 1952, (in part), Univ. Kansas Sci. Bull. 34, pt. 2 (14):936-940.

Diagnosis.—This subspecies closely related to *cortezii* differs from that subspecies and all other subspecies of *P. orbiculare* in having a smaller number of femoral pores (m. 23.8 ∓ 0.8, 14-33), and in having a larger number of spines in the lateral fringe (m. 31.4 ∓ 0.5, 28-36). It differs from all subspecies other than *cortezii* in having a proportionately broader head (HW/HL male m. 1.14 ∓ 0.01, 1.09-1.19; female m. 1.14 ∓ 0.02, 1.05-1.22). *P. orbiculare orientale* has a shorter tail (TL/BL male m. 0.64 ∓ 0.02, 0.55-0.73; female m. 0.55 ∓ 0.01, 0.52-0.61) than *bradti* or *durangoensis* and proportionately longer occipital horns (Occ/BL m. 0.059 ∓ 0.002, 0.045-0.074) than *bradti*.

Type.—No. 19561, a adult male, in the collection of the Museum of Comparative Zoology, was collected by J. Thayer, in 1924 at Miquihuana, Tamaulipas, Mexico.

Description of the type.—The head is much wider than long; its dorsal profile is smooth, its curvature being more acute anteriorly. The supraorbital crest is slightly depressed medially and diverges posteriorly to form an obtuse angle. The nostril is visible from above, facing laterally and forward, on the poorly defined canthal line.

The temporal and occipital horns are well developed and long. The temporal horns project slightly beyond the occipital horns. The occipital horns are about four times as long as the distance between their bases.

The continuity of the lateral fringe is unbroken. The spines of the lateral fringe are about twice as high as wide and are slightly recurved. They are thirty in number.

There are 23 femoral pores. The two series are separated medially by the tip of a single scale. The femoral scales are unnotched behind.

The type has a snout to vent length of 91 mm; the tail length is 62 mm; the ratio of tail to body length is 68 percent. The hind leg is 53 mm long; the ratio of hind leg length to body length is 58 percent. The head width at the angle of the jaws is 23.2 mm; the head length is 19.4 mm; the head width is 119 percent of head length; the supraorbital crest is 13.0 mm. wide; the supraorbital crest width is 67 percent of the head length, and is 56 percent of the head width.

The dorsal surface of the type is light grey, almost silvery white. This color continues onto the tail. Seven crossbands bar the tail, all of which are more or less continuous below. The ventral surface of the type is white. However, the abundance of black mottling almost completely obscures this color. The gular region is particularly heavily mottled, and the chin appears almost solid back.

Size.—The largest specimen, a female, has a body length of 97 mm. The largest male *orientale* has a body length of 91 mm.

Range.—Known from the northern Sierra Madre Oriental in San Luis Potosi,

Tamaulipas and Nuevo León. A single record for the United States is probably not valid.

The range of *orientale* agrees rather well with the Sierra Madre Oriental Biotic Province of Goldman and Moore (1946).

This subspecies intergrades with *cortezii* in southwestern San Luis Potosi (see page 212.

Material examined.—Twenty-eight specimens from 5 localities were examined, as follows:

UNITED STATES. TEXAS: Wilson Co., Sutherland Springs, 1 (MCZ No. 4572).

MEXICO. NUEVO LEÓN: Hacienda Pablillo, near Galeana, 2 (ANSP Nos. 20003, 20031); Ojo de Agua, near Galeana, 3 (CNHM Nos. 30713-30714, 30716). SAN LUIS POTOSI: San Pedro, 4 (ANSP Nos. 20122-20125). TAMAULIPAS: Miquihuana, 80 miles southwest of Victoria, 18 (MCZ No. 17479-17480 and 19560-19565 plus 10 specimens).

PHYLOGENY

The subspecies of *P. orbiculare* are divisible into three subspecies groups. (1) The *bradti* group, including: *P. orbiculare durangoensis* n. subsp. and *P. o. bradti* n. subsp. This group is typified by a narrow head, a small num-

TABLE 1.—Summary of diagnostic characters of subspecies of *Phrynosoma orbiculare*[5]

	Number of specimens male	Number of specimens female	Tail length/Body length male	Tail length/Body length female	Head width/Head length male	Head width/Head length female
bradti	4	6	0.72 ∓ 0.01 0.71 – 0.73	0.62 ∓ 0.02 0.59 – 0.65	1.01 ∓ 0.01 0.98 – 1.03	1.04 ∓ 0.02 1.00 – 1.07
durangoensis	4	7	0.79 ∓ 0.01 0.78 – 0.79	0.63 ∓ 0.03 0.57 – 0.70	0.98 ∓ 0.03 0.95 – 1.01	1.04 ∓ 0.01 1.01 – 1.06
cortezii	22	22	0.62 ∓ 0.02 0.51 – 0.68	0.53 ∓ 0.01 0.43 – 0.60	1.10 ∓0.02 1.02 – 1.19	1.11 ∓ 0.02 1.02 – 1.24
orbiculare	20	16	0.66 ∓ 0.01 0.60 – 0.75	0.56 ∓ 0.01 0.52 – 0.58	1.03 ∓0.02 0.97 – 1.08(1.16)	1.06 ∓ 0.02 0.91 – 1.19
orientale	15	13	0.64 ∓ 0.02 0.55 – 0.73	0.55 ∓ 0.01 0.52 – 0.61	1.14 ∓ 0.01 1.09 – 1.19	1.14 ∓ 0.02 1.05 – 1.22

	Number of Specimens male	Number of Specimens female	Femoral pores	Spines in Lateral fringe	Occipital horn length/ Body length
bradti	4	6	49.0 ∓ 1.3 43 – 55	23.3 ∓ 0.5 21 – 26	0.050 ∓ 0.002 0.045 – 0.057
durangoensis	4	7	41.7 ∓1.6 35 – 46(51)	22.8 ∓ 0.6 20 – 26	0.056 ∓ 0.004 0.044 – 0.071
cortezii	22	22	32.3 ∓ 0.6 24 – 42	28.0 ∓ 0.3 24 –32	0.057 ∓ 0.002 0.042 – 0.078
orbiculare	20	16	31.5 ∓ 0.7 24 – 39	22.9 ∓ 0.4 19 – 28	0.060 ∓ 0.002 0.050 – 0.073
orientale	15	13	23.8 ∓ 0.8 14 – 33	31.4 ∓ 0.5 28 – 36	0.059 ∓ 0.002 0.045 – 0.074

[5] The mean and standard error of the mean are given, followed by the extremes beneath.

ber of spines in the lateral fringe, a large number of femoral pores, a long tail and short to moderately long occipital horns. The *bradti* group occupies the Sierra Madre Occidental from Zacatecas and Jalisco north almost to the Arizona border. (2) The *orbiculare* "group," including *P. o. orbiculare* Linnaeus. A monotypic division containing the typical subspecies, it is characterized by its narrow head, small number of spines in the lateral fringe, intermediate number of femoral pores, relatively short tail and long occipital horns. *P. o. orbiculare* is known from the states of Mexico, Morelos, possibly Tlaxcala and from the Federal District. (3) The *orientale* group, including: *P. orbiculare cortezii* (Duméril and Bocourt) and *P. orbiculare orientale* n. subsp. This is a wide-headed subspecies group with a greater number of spines in the lateral fringe than the other groups, with a tendency towards a reduced number of femoral pores, a short tail length, and a variable occipital horn length. It ranges from the northern Sierra Madre Oriental south to central Vera Cruz, west through San Luis Potosi to the border of the Sierra Madre Occidental, south on the Central Mesa to the edge of the Sierra Madre del Sur. In the Valley of Mexico it is replaced by the *orbiculare* group.

Relationships of the subspecies groups.—Some of the external characters that qualitatively differentiate most members of the genus *Phrynosoma* from the other genera of Iguanidae are the same characters which quantitatively distinguished various subspecies of *P. orbiculare*. They are: body depression (as indicated by head width proportion); spines forming a lateral fringe; tail length and head spines. Considering this we may postulate that the subspecies group which shows the narrowest head, the least number of spines in the lateral fringe, the longest relative tail length and the least development of the head spines is the most primitive. If this is so, the *bradti* group, containing *durangoensis* and *bradti* is the closest to the basal stock.

The subspecies that shows the second greatest number of primitive characters is *orbiculare*. Its narrow head and small number of spines in the lateral series relate it to the *bradti* group, while its long occipital horns, shorter tail and isolated geographic position (relative to the primitive form) mark it as having a long independent evolution.

The remaining subspecies are placed in the *orientale* group. This group is the farthest from the hypothetical common stock of *Phrynosoma*. The *orientale* group has wider heads and more spines in the lateral fringe than both preceding groups. The forms in it further differ from those of the *bradti* group in having a shorter tail.

The bradti group.—Of the two forms, *bradti* and *durangoensis*, the evidence seems to indicate that *durangoensis* is the more primitive. The latter has a higher mean proportional tail length, and has a femoral pore count closer to the number found among other races of *P. orbiculare* and closer to that found among other *Phrynosoma* and that usually found in the other genera of iguanids.

The orbiculare group.—The immediate ancestors of *orbiculare* probably were separated from the stock that give rise to the *orientale* group soon after the separation of the progenitor of the *bradti group*. Once the progenitor of *orbiculare* arrived in the Valley of Mexico it could have been isolated

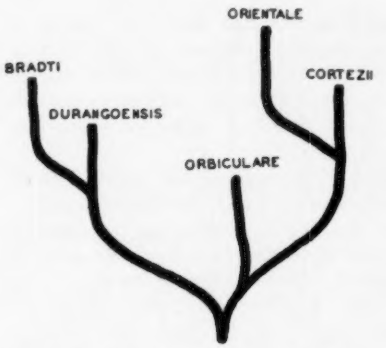

Fig. 2.—A possible phylogeny for the subspecies of *Phrynosoma orbiculare*.

from the remainder of the species either by climatic conditions or by conditions due to vulcanism.

The orientale group.—The two subspecies that form the *orientale* group seem definitely a l l i e d through the characters enumerated above. Inasmuch as the primitive subspecies, of the *bradti* group, have a high number of femoral pores the higher number of femoral pores of *cortezii* probably marks that subspecies as more primitive than *orientale*. *P. o. cortezii* is also more centrally located relative to the other subspecies of *P. orbiculare* than *orientale*.

The preceding remarks on the possible phylogeny of the subspecies of *Phrynosoma orbiculare* may be summarized diagramatically:

KEY TO THE SUBSPECIES OF PHRYNOSOMA ORBICULARE

When utilizing the following key three precautions must be heeded: (1)

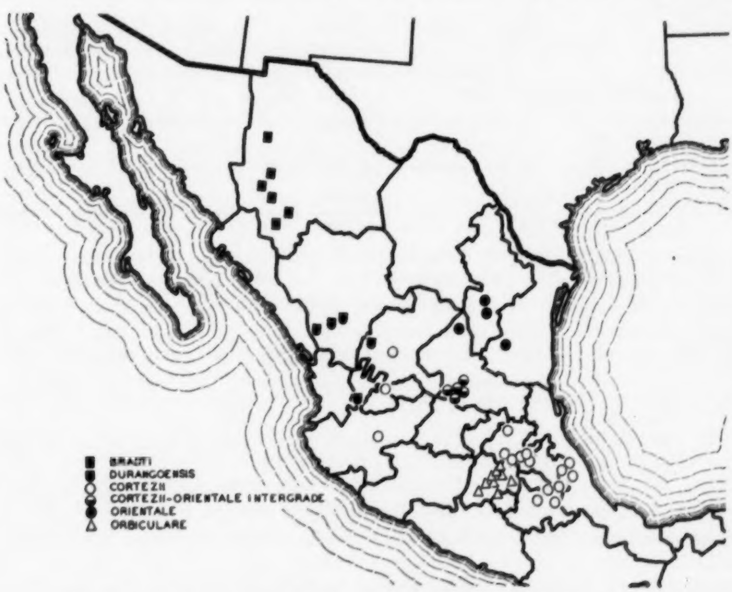

Fig. 3.—The distribution of the locality records of the subspecies of *Phrynosoma orbiculare* examined for the present study. Questionable locality records have not been plotted.

Where the first statement of either a or b applies, that alternative should be chosen. (2) This key will identify most specimens without resorting to proportions, but specimens under 50 millimeters in body length should not be used where proportions are in question. (3) All counts and measurements should be made according to the techniques described under procedure (see pages 205-207).

On the basis of specimens examined 93 percent of all adults and 89 percent of all individuals will be correctly identified with this key.

1a Spines in the lateral fringe more than 32 *or* femoral pores 27 or less .... *orientale*
 b Spines in the lateral fringe less than 28 *or* femoral pores 28 or more 2
2a Femoral pores more than 42 *or* tail length of male more than 70 percent of body length or tail length of female 59 percent or more of the body length 3
 b Femoral pores less than 35 *or* tail length of male less than 70 percent of body length or tail length of female 58 percent or less of body length 4
3a Tail length of male less than 75 percent of body length *or* femoral pores more than 45 in number .... *bradti*
 b Tail length of male more than 75 percent of body length *or* femoral pores less than 45 in number .... *durangoensis*
4a Spines in lateral fringe number 25 or less; head width of males less than 105 percent of head length .... *orbiculare*
 b Spines in lateral fringe number 26 or more; head width of males more than 104 percent of head length .... *cortezii*

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Notes on the Herpetology of the Revillagigedo Islands, Mexico

Bayard H. Brattstrom
California Institute of Technology, Pasadena

The Revillagigedo Archipelago consists of a group of four volcanic, oceanic islands located approximately 210 miles southwest of the tip of Baja California. They are located between 18° 20′ and 19° 20′ N. latitude and 110° 45′ and 114° 50′ W. longitude and are governed by the Mexican state of Colima. The islands, in order of increasing size, are Roca Partida, San Benedicto, Clarion, and Socorro. They are all uninhabited and there is no fresh water on any of the islands except a small stagnant well and some rock seeps on Socorro. The rainy season, according to Hanna (1926), probably occurs from September to December. The only resident vertebrates are birds, introduced sheep (on Socorro Island where they were left in 1867 and are present today only in small numbers), and three species of reptiles. No amphibians or freshwater fishes occur on the islands. No reptiles occur on Roca Partida or San Benedicto islands. The former is a small barren rock and the latter is a steep sided island four miles long and about 2 miles wide. It is on San Benedicto that a new volcano, Boqueron, first erupted in August of 1952 (Williams, 1952; Richards, in press). Clarion Island (6 by 4 miles) is covered with grass and thick clumps of *Convolvulus*-covered prickly pear cactus plus large areas of low shrubs, 5-6 feet high. Clarion island reaches an elevation of 1,000 feet. Its herpetofauna consists of a racer, *Masticophis anthonyi,* a lizard, *Urosaurus clarionensis,* and two sea turtles, *Caretta c. gigas* and *Chelonia mydas agassizi.* Socorro Island (9 by 9 miles) reaches an elevation of 3,710 feet. The dominant vegetation of the west, south and east sides of the island consists of one species of low shrub and a prickly pear cactus. The north side of the island and the elevations above 2,000 feet are covered with broad-leaved tropical plants. The herpetofauna of Socorro consists of one species of lizard, *Urosaurus auriculatus* and one sea turtle, *Chelonia mydas agassizi.*

The islands have been studied biologically only during short stops by major scientific expeditions. Most important of these were the Albatross Expedition (Townsend, 1890) and the California Academy of Sciences Expedition of 1925 (Hanna, 1926; Slevin, 1926). Other expeditions to the islands, as well as the complete history of the islands, can be found in *Mares y Islas Mexicanos del Pacifico,* Mexico, 1949. The reader is referred to Hanna (1926), Johnston (1931), McLellan (1926), Richards (MS), and Brattstrom and Howell (MS) for further descriptions of the islands, their plants, birds, and geology.

In March of 1953, through the generosity of Scripps Institution of Oceanography, I had the opportunity of visiting the Revillagigedo Archipelago during a cruise undertaken primarily to study the geology and volcanology of the islands. The trip was led by Mr. Adrian Richards aboard the Research Ship *Paolina-T,* Robert Newbegin, Captain. The ship left San Diego on March 3

and returned on April 3, 1953. All of the islands were visited; of the islands with reptiles on them, 3 full days and 2 half days (March 14-16, 18-19) were spent on Socorro, and 3 full days (March 23-25) on Clarion Island.

Previously very little had been known about the habits and behavior of the reptiles of the islands and much of this information was obtained on the March trip. The nomenclature used herein is that of Carr (1952) and Smith and Taylor (1945, 1950) and synonymies for the forms used here can be found in these works.

The record of *Hypsiglena torquata ochrorhyncha* collected from Clarion Island by Dr. William Beebe (Bogert and Oliver, 1945) is probably in error. No specimens or signs were seen on Clarion in March, 1953. Bogert has said (personal communication) that it is very possible that the locality data on the one specimen is in error.

CHELONIA MYDAS AGASSIZI Bocourt—Pacific Green Turtle

Green turtles were reported from Clarion Island by Hanna (1926) where he observed them swimming in Sulphur Bay and many others trapped and dying in deep tidepools. In March of 1953, the writer found skeletons of the green turtle well up on the beach of Socorro Island (Hidden Cove) and Clarion Island (Sulphur Bay). Tracks of female sea turtles coming ashore and laying eggs were seen on Socorro (March 18) and on Clarion (March 25). The tracks on Socorro were probably made the night before and were definitely made the night before on Clarion. The tracks seemed to have been made by green turtles. Three live green turtles were seen in Sulphur Cove, Clarion Island on March 24.

CARETTA CARETTA GIGAS Deraniyagala—Pacific Loggerhead Turtle.

While examining the stomachs of the Clarion Island Racer, *Masticophis anthonyi*, I found a very young, and apparently just hatched, *Caretta c. gigas*. This proves to be the first record of loggerhead turtles from the Revillagigedo Islands and shows that they definitely breed on Clarion Island.

MASTICOPHIS ANTHONYI (Stejneger)—Clarion Island Racer.

Masticophis anthonyi is a fairly thick bodied, dark brown racer with occasional black flecks on the head and on each scale of the back, becoming less flecked on the sides. The belly is white, gray, or tan and occasionally flecked with black. The lateral edges of the ventrals are tipped with brown. A full description of this species can be found in Ortenburger (1928). The longest specimen caught on the March trip was 1362 mm. The type specimen is 1450 mm long (Stejneger, 1901). Ortenburger (1928) noted that this species was the oiliest and fattest of all of the species that he examined. All specimens collected in March, 1953, contained large fat bodies. *M. anthonyi* is found only on Clarion Island.

Slevin (1926) records these snakes as "A common species about sea bird colonies and cactus patches in the vicinity of Sulphur Bay, Clarion Island." Other than this, little was known of their natural habits. I found these snakes common in all types of habitats available on Clarion Island. They were observed from the coral and lava beach to the top of the highest point, Mt. Gallegos. For shelter they seemed to prefer rocky areas covered or surrounded

by cactus, but they usually foraged away from these rocky areas and as a consequence they were often flushed in the open grassy areas. If frightened they would dash to a cactus or rocky area and thus escape capture unless the pursuer charged into the spiny cactus.

When caught, this racer, unlike most others, does not bite or even hiss. The snakes seemed most active in the morning (7:50 to 10:25 A.M.) but were usually active at any time that the sky was overcast with altocumulus or stratocumulus clouds. Though usually on the ground, Slevin (in Ortenburger, 1928) records that sometimes they were seen stretched out on top of the low growing cactus, sunning themselves.

Slevin (in Ortenburger, 1928) thought that the snakes ate baby birds (boobies, doves, and wrens) and lizards. This is supported by Ortenburger (1928) who found a bird feather and a lizard (*Urosaurus clarionensis*) in one individual. I found food in only one specimen and this was the young loggerhead turtle as stated above. No parasites were found in any of the specimens examined.

Temperature data on five specimens is given below. The optimum body temperature is near 29.9°C and the lethal temperature (unfortunately based on only one experiment) is 40.5°C.

Temperature °C			Time of Day
Soil	Air	Body	
25.2	25.5	25.0	7:50 A.M.
31.0	25.0	27.0	9:15 A.M.
29.8	25.5	25.0	10:25 A.M.
29.5	24.0	34.0	2:15 P.M.
29.4	24.0	34.0	2:55 P.M.

UROSAURUS AURICULATUS (Cope)—Socorro Island Rock Lizard.

Urosaurus auriculatus is a fairly large, smooth-scaled, bluish lizard. The females are smaller than the males and are not as blue. In the adult male, the head, legs, tail, belly, and mid-dorsal area are blue. There are 10 dorsoventral vertical black bands on each side tending to encroach upon the dorsal blue area. The legs and tail have black cross bands and there is a small λ-shaped black blotch descending from one of the vertical bars to a point in front of the fore leg. Of 22 specimens caught in March, the snout-vent measurement varied from 35 to 67 mm (average 45.7) with a tail a little more than twice the snout-vent length. Head lengths varied from 10 to 15.5 mm (average 11.6). The femoral pores varied from 9 to 12 per side (average 10.1). Slevin (1926) records the femoral pores of 20 individuals varying from 10 to 13 (average 11.1). The testes (in alcohol) of an adult caught in March measured 4.4 mm long and appeared to be regressive, although no histological sections were made.

Slevin (1926) records that "This species, the only one found on Socorro Island, ranged from sea level to about 2,500 feet, but only one or two specimens were found at this elevation." In March, these lizards were found on all parts of the island from sea level to the top of Mt. Evermann (3,710 feet), the highest point on the island. It was very common in the open rocky or grassy areas just behind the beaches, tidepools, or sea cliffs, though as Slevin

(1926) states, it was "A common but not an abundant species." It is definitely less abundant in most of the bushy areas of the island where the cactus and shrubs are so dense that there are only a few open spots. It seems to be quite an adaptable species as it was found in cracks in rocks, under debris on sandy beaches, in piles of lava boulders, under rocks on the ground, and, higher in the island, crawling about in trees. In this regard it differs from *U. clarionensis* which is primarily a rock dweller. Occasionally *U. auriculatus* was found on rocks just behind the sea spray.

All the lizards on Socorro were wary and difficult to collect though the birds on the island were unafraid of man. It is possible that this results from the predatory activity of the resident subspecies of red-tailed hawk (*Buteo jamaicensis socorroensis*), which was occasionally seen flying low over the lower parts of the island. There are no mammals on the island for the hawks to feed on. The male *U. auriculatus* seemed to be more numerous than the females and of the 22 specimens caught, 18 were males. The female is smaller and browner than the male and perhaps escapes the detection of the collector. These lizards were usually first seen while running from rock to rock or bush to bush, whereas *U. clarionensis* was usually first sighted sitting on top of a large lava boulder.

Urosaurus auriculatus seemed to be active most of the day except during the mid-day. The lizards would usually bask on the rocks in the sun for only a few seconds or minutes at a time and more often they would sit on a rock in the semi-shade of a bush. No evidence of territoriality or aggressive behavior was noted in any case and it is most likely that the breeding season was over. The same was noted for the birds of Socorro (Brattstrom and Howell (MS).

Stomach contents show that the food of *U. auriculatus* consists primarily of ants and spiders, with other insects and flowers often taken. Insects were less in evidence on Socorro than on Clarion and most of the annuals had finished blooming. Sand was found in only one specimen. Parasites (intestinal nematodes) were found in 14 out of 22 individuals. These are being studied by Read (MS). The high degree of parasitism (63%) is probably associated with the large number of plants eaten by this lizard (Read, MS). The food of *U. auriculatus* and *U. clarionensis* is compared in tables 1 and 2.

With air temperatures varying from 22 to 34°C and soil temperatures varying from 23 to 43°C, body temperatures of active *U. auriculatus* varied from 32.2 to 39° (25 lizards) the optimum temperature is near 36.3°C (19 lizards). Two lizards (at 6:45 A.M. and 5:30 P.M.), one in a hole and the other under some debris on the beach, had body temperatures of 25.2° and 24.5°C respectively.

Experiments performed in Los Angeles indicate that the lethal temperature (9 trials, range from 42.5 to 44.5°C) is 43.5°C compared to 41.8°C for *U. clarionensis*.

UROSAURUS CLARIONENSIS (Townsend)—Clarion Island Rock Lizard.

This lizard is very abundant on Clarion Island, to which it is restricted. The male is bright green with irregular lateral black markings. The females are smaller than the males and are brown above but with some green on the sides. Townsend (1890) and Van Denburgh (1922) report the color of the

lizard as blue, like that of *U. auriculatus* on Socorro Island. This was corrected by Slevin (1926), who reported that the lizards are green, suggesting that Townsend's and Van Denburgh's information was based on specimens in alcohol, as the green fades to blue in alcohol. Mittleman (1942) repeated Townsend's mistake and described the lizard as bluish.

The male does not appear brilliant green unless its body temperature is above 26°C (as determined in the laboratory). Below 26°C it is brownish yellow with the same black markings. Even when excited, while its body temperature is below 26°C, it does not change to green. Temperature is probably the primary color control in this lizard and not adrenalin (see Atsatt, 1939).

Urosaurus clarionensis is one of the spiniest of this genus and resembles at first (except for the green color) a small *Sceloporus*. The back, sides, legs, belly, head, and tail of the adult male are green. There is a Y-shaped black shoulder patch. The lower part of the Y passes ventrad to a point in front of the fore leg. There are 2½ rows of small lateral black blotches on each side. The legs and tail are green and are barred with black. Snout-vent measurements vary from 29 to 60 mm (average 48.5 mm based on 44 individuals, omiting the juvenile with a snout-vent measurement of 29 mm). Head lengths of 42 individuals varied from 8 to 16 mm (average 13.1 mm omitting the same juvenile). The tail length is just a little more than two times the snout-vent length. Femoral pores in 43 specimens varied from 9 to 14 (average 12.0) per side. Slevin (1926) records the femoral pores of 20 specimens varying from 10 to 14 with an average of 12.1 per side. Of 47 lizards collected in March, 42 were males and 5 were females. The small size of the female and their brownish coloration probably accounts for their not being seen by the collector as easily as the bright colored males. Testes (in alcohol) measured from 3.0 to 3.5 mm in length in a few individuals. They seemed small, possibly regressing, though no histological sections were made.

Slevin (1926) records this lizard as ". . . confined strictly to the lower levels as none were observed on the plateau or higher parts of the island." In March of 1953, however, the lizards, as well as the racer, were found to be common all over Clarion Island from sea level to the top of the highest peak, Mt. Gallegos (1,000 feet, approx.). It appeared to be restricted primarily to large (3 to 10 feet high) lava boulders which were common about the slopes of the island. The male lizard is very conspicuous sitting on the top (as was usual) or the side of the large black boulders. A few juveniles were seen and caught on a gravel area with low annual plants and morning glory vines just behind the beach of Sulphur Bay. No lizards were found in the open grassy areas with no boulders on them, nor were they found on the two dry, non-vegetated "lagoons" on the island. These "lagoons" probably hold water temporarily during the rainy season.

Like the wrens on Clarion Island, the male lizards were observed to defend their territories from other males. This is in contrast to the behavior of the birds and lizards on Socorro Island. Occasionally a male and a female *U. clarionensis* were observed crawling about on the same rock and territories seemed well established. *Urosaurus clarionensis* seemed to be more active reproductively than *U. auriculatus* from Socorro Island. This was also noted in regard to the passerine birds of the island and it is possible that the breed-

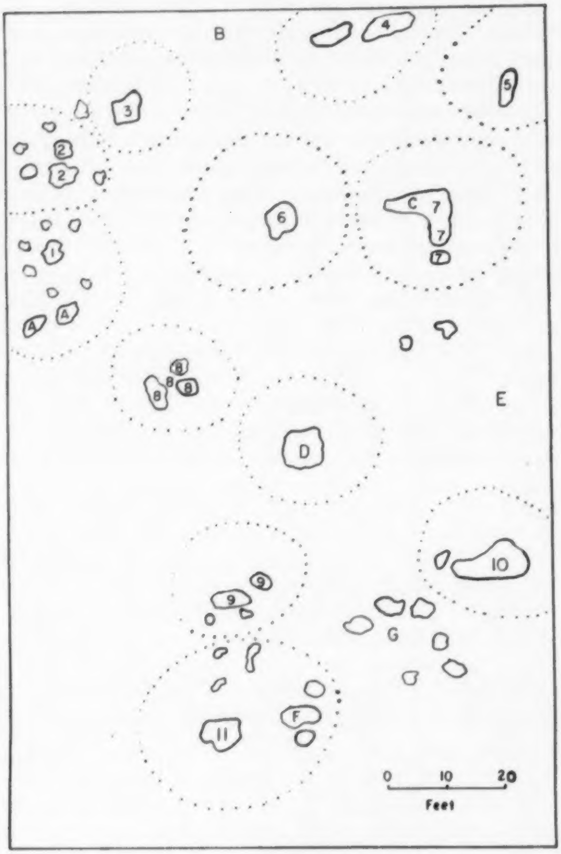

FIG. 1.—Diagram of the area on the south side of Clarion Island where territorial observations were made on *Urosaurus clarionensis*. Numbers represent males and letters represent females. The irregular shaped objects are lava boulders and the dotted lines indicate roughly the area of activity of each male lizard as drawn from the lizard's center or main rock.

ing season on Socorro is earlier than it is on Clarion. It may occur on each island just after the rainy season (August to December according to Hanna, 1926). Photoperiodism is probably not an important factor as the islands are well within the tropics.

On the south side of Clarion Island, which consists of a gentle slope from the top plateau of the island to the ocean, the writer observed *U. clarionensis* in an area where the grass was very low (up to one foot high) and with only a few small low bushes and vines. In this area there were a large number of large boulders 2 to 6 feet high and many smaller boulders. By watching and walking through the area in all directions, it was possible to observe the posi-

tions of all the lizards. The lizards were not too wary and from any point in the area almost all of the lizards could be seen and their movements recorded. The area was observed for about 2 hours in the afternoon (3:00 to 5:00 P.M.) of March 25. Obviously in such a short time the animals did not move about much, but by observing lizards in the area and elsewhere on the island, it was noted that the lizards sat on one main rock, which was roughly in the center of its territory or home range. From this main rock, the lizards would wander about in search of food. Occasionally the lizard would get on top of a small rock, but more often it would return to the center rock. Other foraging trips would be either in the same or another direction, but always returning to the center rock. By mapping the rocks and lizards, as in fig. 1, the centers of activity of the lizards could be determined by the above means, together with population density and home range size. It is not known if there is an undefended home range as well as defended territory.

Arbitrary boundaries were given to a small section of this south slope of the island. This area was 88 feet wide and 145 feet long. The long axis ran up and down the gentle slope (i.e., north and south). In this area there were 27 large boulders and many small rocks. A total of 8 females and 11 males were observed. This would give, if equally divided, 1,160 sq. ft. per male or 671.6 sq. ft. per individual. By walking back and forth in the area it was possible to observe and count all the individuals. In the first 15 minutes about 15 lizards were sighted. In the next 15 minutes the remaining 4 were observed. No additional lizards were seen in the area in the next 1½ hours, though all the lizards were active during the two hours of observation.

The females seemed to be in the same territory as the male in two cases (once on the same rock) and in separate territories or areas (i.e., areas with no males) in 5 cases. If, as the facts suggest, the reproductive season was over (i.e., testes probably regressing, no eggs in the female, small numbers of juveniles found, etc.) the females had probably finished laying eggs and did not necessarily remain in the presence of a territorial male, but were wandering about looking for food (see Fitch, 1940; Stebbins, 1944; and Stebbins and Robinson, 1946). It is possible that in some cases the females became slightly territorial themselves (fig. 1, D, E, F, and G) or at least had home ranges to themselves. Whether these were defended or not is unknown.

All the males seemed to be territorial and some aggressiveness and defense of territory was noted. As seen in fig. 1, the male *U. clarionensis* were from 15 to 60 feet apart. The average distance between the center of the territories is about 30 feet so that each lizard has an area of roughly the shape of a circle 15 feet in radius or an area of approximately 706 square feet. This is, of course, modified by local topography. For instance, lizards 1, 2, and 3 are only 15 feet apart at the centers of their territories whereas 4, 5, 6, and 7 are 25 to 40 feet apart. In this case, 1, 2, and 3 are in areas of many small boulders most of which are under 15 inches in diameter, while 4, 5, 6, and 7 are centered about large boulders up to 6 feet high with no or few small boulders in between.

In contrast to the activity of the Clarion Island racer, the *U. clarionensis* were not very active during the cloudy or partly cloudy parts of the day. When the clouds started breaking up at about 10:00 A.M. each day, the lizards

became more active and this activity continued through the rest of the day. It did not subside during mid-day as in the case with Socorro. This is probably due to the fact that on Socorro the low elevations are almost always free of clouds and fog and the temperatures get very high in the day, approaching the conditions found in the deserts. The clouds may remain about the top half of Socorro Island all day. In the case of Clarion Island—at least during the time spent there—clouds formed about the island in the late afternoon and did not clear up until about 10:00 each morning. Although air temperatures on Clarion were high, they never were as high as those on Socorro.

The Clarion *Urosaurus* were never as wary as the *U. auriculatus* on Socorro. The droppings and pellets of the resident ravens and burrowing owls on Clarion showed no trace of lizard remains. Ortenburger (1928) records *U. clarionensis* from the stomach of the Clarion racer, *Masticophis anthonyi*. This may be one of the reasons for the preference of the higher rocks by the lizards.

When escaping from the collector, the individuals of the Clarion *Urosaurus* usually ran into holes or cracks between the large lava boulders and the ground.

A summary of the food of *Urosaurus clarionensis* is presented in tables 1 and 2. The food of this lizard consists primarily of spiders, grasshoppers, hemipterans, homopterans, and ants. During March the insects and spiders were definitely more abundant on Clarion than they were on Socorro. Although there were many bees and wasps on Clarion, these were found in only two stomachs. The grasshoppers and spiders were in great abundance on Clarion and the grasshoppers furnished food for the Clarion Island burrowing owl as well as the lizards. The large number of membracids in the stomach is unusual for lizards, but what is more unusual is the pentatomids. The mainland forms of these "stink bugs" are known to have a disagreeable odor and hence are seldom eaten by lizards. These, however, were fairly common in the stomachs of *U. clarionensis*.

The degree of parasitism is very low in *U. clarionensis*. Parasites (intestinal nematodes) were found in only 3 individuals (7.5%) compared to 63% for *U. auriculatus*. This probably results from the fact that *U. clarionensis* is less herbivorous than *U. auriculatus*, as the lizards are infected by eating plants. The parasites are being studied by Read (MS).

With air temperatures varying from 23.2° to 32°C and soil temperatures varying from 25° to 50°C, body temperatures of active *U. clarionensis* varied from 29.6° to 39°C (59 individuals) with the optimum temperature near 36.4 (37 individuals). The lowest tolerable temperature appears to be 29.6°C. Experiments in the laboratory indicate a lethal temperature of 41.8°C (6 tests, range 40.5° to 44.5°C).

TABLE 1.—A comparison of the contents of the digestive tract of *Urosaurus auriculatus* and *U. clarionensis*. Number and percentage containing different types of material.

	No. examined	Animal matter		Plant matter		Parasites (Nematodes)	
		Number	%	Number	%	Number	%
auriculatus	22	22	100	8	36.4	14	63.6
clarionensis	40	40	100	1	2.5	3	7.5

TABLE 2.—A comparison of the food of *Urosaurus clarionensis* and *U. auriculatus.* Numbers indicate number of individuals in which a particular item was found. The first column refers to *auriculatus* and the second to *clarionensis.*

		FOOD ITEM (animal)			
Lizard skin	2	....	Insects (continued)		
Spiders	9	20	Lepidoptera		
Oribatid mites	1	....	Larvae	4	3
Centipedes	1	....	Moths	1	1
Sowbugs	2	....	Diptera (unidentified)	....	1
Insects			Coleoptera		
Unidentified	9	7	Tenebrionidae	2	....
Orthoptera			Carabidae	2	....
Locustidae	....	12	Coccinellidae	....	4
Cryllidae	....	1	Hymenoptera		
Hemiptera			Unidentified	4	....
Unidentified	1	2	Formicidae	21	9
Pentatomidae	....	5	Chalcidoidea	1	....
Homoptera			Specidae	....	1
Unidentified	1	....	Apoidea	1	1
Cicadellidae	3	....	Megachilidae	....	1
Membracidae	....	8	Unidentified larvae	9	....
		FOOD ITEM (plant)			
Leaves and stems	4	....	Unidentified tissues	1	....
Flowers and parts	7	....	Seeds	....	1

ORIGIN OF THE FAUNA

Slevin and Hanna (in Hanna, 1926) came to the conclusion that the reptiles, passerine birds, and plants (but see Johnston, 1931 for the plants) reached the islands during a previous connection with either the mainland of Mexico or Baja California. This is based on Hanna's discovery (1925, 1926) that from a boat's-length away, Roca Partida, the smallest of the Revillagigedo Archipelago appeared granitic. On the March, 1953 trip the geologist, Mr. Adrian Richards of Scripps Institution of Oceanography, managed to land on the dangerous rock and obtained rock samples to prove that this, like the other three islands, was not granitic but volcanic. The submarine and surface geology of the islands (Richards, MS) shows that the islands are all oceanic and volcanic and independently rise from an ocean floor of about 2½ miles depth. There are no interconnecting ridges between the various islands nor between the islands and the mainland (Richards, MS). Faced with this evidence, we can explain the origin of the herpetofauna only by means of floating debris or rafts. Other possibilities such as lizards in the bill or feet of birds seems unlikely because of the distance to be traveled. The turtles are marine and pelagic and pose no problem. The lizards and the racers appear to be independent chance arrivals on the islands by means of rafts.

Roca Partida is very small (300 feet long and 110 feet high) and has no life on it except nesting sea birds. It is not suitable for habitation by any terrestrial animal or plant. San Benedicto had, prior to the eruption of the new volcano, a flora of 10 species of plants (Johnston, 1931) and only one bird, the San Benedicto rock wren. The sides of San Benedicto island are very steep cliffs from 60 to 100 feet high, and originally without beaches, although

there are beaches now as the result of ash from the volcano. Chance raft arrivals to this island would not be able to become established on the island even though they reached its base. Socorro and Clarion islands, however, are low and large and have a large flora and fauna. It is on these two islands that the reptiles are found. Geologically, Clarion Island is the oldest of the four islands with Socorro and San Benedicto next in order. Roca Partida is just a remnant of a former island and is too small to indicate its age (Richards, MS). The geological age of the islands is unknown but the evidence indicates a possible Miocene origin of Socorro and Clarion. On the basis of the differentiation of the reptiles from their closest relatives, it is believed that the reptiles reached Socorro and Clarion in the early Pliocene.

Ortenburger (1928) believed that *Masticophis anthonyi* was derived from *Masticophis lineatus* (=*M. f. lineatus*). The latter was derived from the basal stock of the *M. flagellum* group, namely *M. f. flavigularis* (=*M. f. testaceus*). *M. lineatus* apparently gave rise to both *anthonyi* and *mentovarius*. Assuming that the ranges of the species have not greatly changed and that the center of dispersal of the *flagellum* group was in the plateau region of Mexico, it appears that *M. anthonyi* was probably derived from the west coast of Mexico, probably southern Sinaloa, Nayarit, or Colima.

Urosaurus clarionensis and *U. auriculatus* are more closely related to mainland forms than they are to each other. They are placed by Mittleman (1942) in different groups of *Urosaurus* as the most primitive members of their respective groups. Both of the Revillagigedo species were apparently derived from *Urosaurus ornata schotti* (*Uta ornata lateralis* Boulenger, *cf.* Oliver, 1943) and hence have their closest relatives today in southern Sonora and Sinaloa. All three reptiles have their closest relatives in western Mexico. It is most probable therefore, that the terrestrial reptiles of the Revillagigedo islands were derived from the west coast of the Mexican mainland and not from Baja California. They apparently reached the islands independently by rafts and it is suggested that this probably occurred in the early Pliocene.

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Contribution to the Herpetology of Sonora, Mexico:

Descriptions of New Subspecies of Snakes (Micruroides euryxanthus and Lampropeltis getulus) and Miscellaneous Collecting Notes

Richard G. Zweifel and Kenneth S. Norris

Museum of Vertebrate Zoology,
University of California, Berkeley and Scripps Institution of Oceanography, La Jolla

The basis for this report lies largely in a collection of reptiles and amphibians made in Sonora by the authors in the course of three trips to that state. During late January and early February, 1950, the junior author obtained a few turtles incidental to fish collecting. At the same time, the senior author accompanied William G. Reeder south as far as Guirocoba, Sonora. On this latter trip, about 75 lizards and frogs were collected, all in the southern portion of the state.

In August, 1950, the authors accompanied by Mr. Reeder, journeyed south to Guirocoba where two weeks were spent. Although some of the 123 amphibians, 123 snakes, 184 lizards and 21 turtles taken on this trip were obtained enroute between Guirocoba and the International Boundary, the vast majority came from Guirocoba. The size of the Guirocoba collection is a tribute to the ability of the native collectors, since climate and bacilli combined to reduce greatly the gringo's efficiency. Bogert and Oliver (1945) have provided a description of Guirocoba. Briefly, it lies in the Tropical Deciduous Forest about 28 miles by road east southeast of Alamos.

Dr. L. M. Klauber has kindly made available to us Sonoran reptiles in his own personal collection and in the collection of the San Diego Society of Natural History. These collections have yielded several new records for the state. A small collection from the vicinity of Guaymas was kindly donated to us by A. A. Allanson of Scripps Institution of Oceanography. Another small but valuable collection was presented by Mr. Sterling Bunnell of Berkeley, California.

Acknowledgments.—We are indebted to the following persons and institutions for the loan of specimens in their care (abbreviations used in this paper are indicated in parentheses): Charles M. Bogert, American Museum of Natural History (AMNH); Dr. Doris M. Cochran, United States National Museum (USNM); Dr. R. B. Cowles, University of California, Los Angeles (UCLA); Dr. Laurence M. Klauber, San Diego Society of Natural History (LMK and SDSNH); Dr. C. H. Lowe, Jr., University of Arizona (UA); Dr. G. S. Myers, Jay Savage, Stanford Natural History Museum (SNHM); Dr. Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); and William Woodin III, Tucson, Arizona (WW). Where no museum abbreviation is cited, the specimens are in the Museum of Vertebrate Zoology, University of California, Berkeley. We are especially grateful to Mr. Clay Montgomery for the use of the facilities of Rancho Guirocoba.

Accounts of Species

Scaphiopus couchi Baird

15.8 mi. S Hermosillo (50518); 23.8 mi. S Hermosillo (50519-20); Guirocoba (50521-24).

The specimens captured near Hermosillo were calling from roadside

rainpools on the evening of August 3, 1950. They were floating in the center of the pond with throat pouches inflated. The Guirocoba specimens were found beneath surface litter and hopping about on the ground at night. No breeding activity was noted during the period of our stay at Guirocoba (August 6-19).

A considerably darker ground color is present in the Guirocoba specimens as compared to those from near Hermosillo. In addition, the southern specimens are smaller and possess less extensive webbing on the hind feet. They resemble those described from Sinaloa by Taylor (1936b) in that the skin of the head is co-ossified with the cranium even in the smallest individual, snout-vent length 41 mm. There also seem to be pattern differences, but these cannot adequately be demonstrated without comparing living material.

BUFO ALVARIUS Girard

18.4 mi. N Hermosillo (50558); Giurocoba (50559-61, 50563).

A number of these large toads were observed at night on the highway during and after thundershowers on August third. An individual from Guirocoba was found at night in a water-filled pothole in an arroyo.

BUFO HORRIBILIS Wiegmann

Guirocoba (50564-5).

Of the two large toads present at Guirocoba, *B. alvarius* was considerably more common than *B. horribilis*. A sufficient number of specimens was not secured to enable us to determine if there were any differences in habitat preference between the two forms.

BUFO MAZATLANENSIS MAZATLANENSIS Taylor

Guirocoba (50538-57); Arroyo Cuchujáqui, 8 mi. SE Alamos (SDSNH 18860).

Both *Drymarchon corais rubidus* and *Thamnophis cyrtopsis* were found to have fed upon this species of toad, the most abundant *Bufo* at Guirocoba.

BUFO PUNCTATUS Baird and Girard

23.8 mi. S Hermosillo (50509); Guirocoba (50510-12); 2 mi. W Bahia Santa Rosa, east side of Tiburon Island (20683).

The individual taken near Hermosillo was calling from a roadside rainpool shortly after a thundershower on the evening of August third. On August 12, at Guirocoba, large numbers of newly transformed toads were found in the daytime hopping about on dry ground in the Tropical Deciduous Forest.

At Guirocoba, *Drymarchon* was found to have fed upon this toad.

The Tiburon Island specimen, collected April 4, 1936 by S. B. Benson, was found during the daytime in a small, nearly dry tinaja. It seems to be the first recorded for that island.

LEPTODACTYLUS MELANONOTUS (Hallowell)

Guirocoba (50403-42); Alamos (52039-46); 1 mi. SW Hermosillo (26066).

Smith and Taylor (1947) have listed both *L. melanonotus* and *L.*

occidentalis from Sonora. Most of our Guirocoba specimens, taken in midsummer, possess well developed dark brown horny areas in the lateral pectoral and post-femoral regions and have well defined post-tympanic glands. In these respects they agree with *L. occidentalis* Taylor. But some Guirocoba specimens lack horny areas, or have them only slightly developed and also have ill-defined post-tympanic glands. A comparison of the two groups, by sexes, with respect to tibia length/snout-vent length ratio and snout-vent length showed no statistically significant differences between the two groups, nor are there discernible differences in color or pattern.

The specimens from Alamos were taken in the winter and show little or no development of the horny areas. Bogert and Oliver (1945) found that their Alamos material, taken in the summer, had these areas well developed, while their Guirocoba specimens, also summer collected, did not. Our material shows, as did Bogert and Oliver's, that the development of the horny areas is independent of both sex and breeding condition and that a graded series from one extreme to the other can be found in frogs from one locality, hence we refer them all to one species, *L. melanonotus*. While it may eventually be possible to recognize a distinct Pacific Coast form to which the name *L. occidentalis* Taylor is applicable, we do not feel that it has yet been sufficiently defined to permit its recognition.

Leptodactylus melanonotus was the most abundant anuran at Guirocoba. At night during the summer, these frogs gave their short, snapping call from the shelter of streamside grass and flood-washed debris along a cypress (*Taxodium mucronatum*) bordered stream. The black tadpoles were common in shallow areas in streams and had the habit of congregating in compact groups on the bottom.

The individual from one mile southwest of Hermosillo was captured in a roadside irrigation ditch on May 17, 1936. This record extends the known range 180 miles to the northwest.

PTERNOHYLA FODIENS Boulenger

Guirocoba (50462-74).

Only one of the thirteen specimens is an adult. This one (snout-vent length 57 mm) was removed from the stomach of a *Leptophis diplotropis*. To judge from our specimens, coossification of the skin of the head with the cranium begins at about 29 mm s-v length and is complete at about 33 mm, with some individual variation.

HYLA BAUDINI (Duméril and Bibron)

Guirocoba (50443-61).

Numerous young and newly transformed individuals were found in August at the edge of a stream which flows through the Tropical Deciduous Forest at Guirocoba. They were found in shallow water among aquatic plants. One adult had been eaten by a *Leptophis diplotropis*.

AGALYCHNIS DACNICOLOR (Cope)

Guirocoba (50392-402).

On the night of August 15, several *Agalychnis* were collected along a small stream which flows through a cultivated valley at Guirocoba. When frightened, these frogs leaped from the grassy bank into the water, but

did not seek refuge there, merely swimming slowly to the opposite bank and climbing out again. A mass of frog eggs found on the grassy bank about one foot above the water, much as described by Taylor (1942) was presumably of this species.

The only *Agalychnis* seen active in the daytime was the object of an attack by a *Leptophis diplotropis*.

RANA PIPIENS Schreber

Arroyo Cuchujáqui, 8 mi. SE Alamos (UCLA 4797-4807, MVZ 52032-52038); Guirocoba (50505-08).

On the evening of February 5, 1950, these frogs were found to be very abundant along the Arroyo Cuchujáqui. Breeding activity was going on at this time and evidently had been in progress for some weeks, since eggs, transforming larvae, and all intermediate stages were present. The adult frogs were in full chorus at night and some continued to sing throughout the day from the shelter of flood-washed debris bordering the stream. Water temperatures taken at night where the frogs were found calling or in amplexus varied from 20.0 to 20.8°C.

The area was revisited on August 19, but no *Rana* was observed, nor were any tadpoles seen although a number of seine hauls for fishes were made. It may be that in this region the breeding season is limited to the period of gentle winter rains, thus avoiding the abrupt changes of water level characteristic of the summer rainy season.

PHYLLODACTYLUS HOMOLEPIDURUS Smith

Agua Marín, 8 mi. WNW Alamos (UCLA 4319-22, MVZ 50566); Guirocoba (50567-9).

On February 2, 1950, four geckos were found beneath loose bark on a dead tree standing in the middle of the wash in Aqua Marín Canyon. In the evening, many more were observed in cracks in granite outcroppings at the same locality, where the surface temperature of the rock ranged from 21.5 to 27.5°C. On August 5 an adult gecko was shot in a crevice of an overhanging branch of a large fig tree at the same locality. This was unusual in that the lizard was active in the daytime, though in the shade. Individuals at Guirocoba were seen on the adobe walls of the ranch buildings.

Phyllodactylus is considered by the Mexicans to be very poisonous, so much so that even touching one is believed to cause sickness or death. The Mexicans frequently attribute infant mortality to this lizard.

ANOLIS NEBULOIDES Bocourt

Agua Marín, 8 mi. WNW Alamos (28789); Arroyo Cuchujáqui, 8 mi. SE Alamos (UCLA 4288-9); Guirocoba (28786, 28788, 50570-73).

Two females, s-v length 39.2 and 40.2 mm, collected at Guirocoba on August 8 and 16, 1950, each contained two eggs measuring 5x10 mm.

The dorsal pattern is variable. One of the Arroyo Cuchujáqui specimens possessed a well defined bronze dorsal band which contrasted markedly with the dull gray-brown of the dorsal surface. In the other specimens this marking was obscure or absent. In both males and females, the gular pouch area is pale pink in life.

Specimens collected by us were found on the main stems of bushes from two to five feet above the ground. Another was found on the trunk of a cypress (*Taxodium mucronatum*).

CTENOSAURA HEMILOPHA (Cope)

Guirocoba (50850-62)

Adults of this species were commonly observed in dead trees and on rock walls. The Mexicans of Rancho Guirocoba believe that the iguanas of the trees and walls represent two different kinds, those in the trees being edible and the others inedible. The edible tree iguanas are supposed to act as an aphrodisiac when eaten. An iguana eaten by us produced no effect.

In contrast to the adults, the brilliant green juveniles are not so restricted in habitat, and are often seen on the ground.

HOLBROOKIA MACULATA THERMOPHILA Barbour

35.2 mi. S Hermosillo (50591-2); Guirocoba (50593-634).

The Hermosillo specimens were taken in the mesquite-grass association. At Guirocoba the lizards were abundant in open areas bordering the thicker growth.

CALLISAURUS DRACONOIDES VENTRALIS (Hallowell)

6.7 mi. N Gonzalitos (50574).

CALLISAURUS DRACONOIDES BREVIPES Bogert and Dorson

12.4 mi. NW Navajoa (50575); 3 mi. NW Navajoa (UCLA 4275); Agua Marín 8 mi. WNW Alamos (UCLA 4276-8); Alamos (UCLA 4279-82); Arroyo Cuchujáqui, 8 mi. SW Alamos (UCLA 4283-4); Guirocoba (50576-90).

Where vegetation is thick, these lizards tend to be most common in open areas such as sandy washes or bare expanses of sandstone.

When they take alarm the tail is curled over the back and waved slowly from side to side before the animal runs.

PHRYNOSOMA M'CALLI Hallowell

10 mi. NE Punto Penasco (LMK 38333); 7½ mi. NE Punto Peñasco (LMK 38552).

This lizard has been reported from Sonora from the "East bank of the Colorado River, 5 miles south of the United States border" (Smith and Taylor, 1950: 100). The present records extend the known range about 100 miles to the southwest.

PHRYNOSOMA PLATYRHINOS CALIDIARUM (Cope)

22 mi. SW Sonoyta (LMK 37732); 16 mi. NE El Papalote (LMK 38518); Sierra del Piñacate (LMK 38058-9); 12½ mi. SW (LMK 38520) and 14 mi. SW Pozo Sipiano (LMK 38432); 3 mi. E Las Chollas Point (LMK 38517, 38267).

The presence of this northern race in extreme northwestern Sonora, rather than *P. p. goodei* as mapped by Reeve (1952), conforms to the pattern of distribution of several other reptiles, in which the race of the Colorado Desert ranges south and east into and beyond the Punta Penasco region.

PHRYNOSOMA SOLARE Gray

6.7 mi. N Gonzalitos (50708); ½ mi. N Gonzalitos (50709); 27 mi. NW Navajoa (50710); Guirocoba (50711-13); 7 mi. NE Magdalena (LMK 39871).

The *camaleon* is one of the less common lizards at Guirocoba, represented by only three specimens among 184 lizards secured there.

SCELOPORUS CLARKI BOULENGERI Stejneger

15 mi. E. Navajoa (UCLA 4348); Alamos (UCLA 4349; Arroyo Cuchujáqui, 8 mi. SE Alamos (UCLA 4350); Guirocoba (UCLA 4347, MVZ 50638-76).

The Arroyo Cuchujáqui specimen was found on a tree trunk. One adult had been eaten by a *Masticophis flagellum piceus*.

SCELOPORUS NELSONI Cochran

Agua Marín, 8 mi. WSW Alamos (UCLA 4267-9, MVZ 50697); Guirocoba (UCLA 4270-74, MVZ 50698-707).

All nineteen specimens were collected in rocky and bushy areas in canyon bottoms in the Tropical Deciduous Forest. None was seen outside of this habitat.

UROSAURUS GRACIOSUS Hallowell

12 mi. NE Punto Penasco (LMK 38545).

This species has not previously been recorded from Sonora, though it probably occupies most of the region mapped by Shreve as the Lower Colorado Valley (Shreve 1951, map 1).

UROSAURUS ORNATUS LATERALIS (Boulenger)

3 mi. NW Navajoa (50922-26); 5 mi. E Navajoa (50928); 10 mi. E Navajoa (50927); Agua Marín, 8 mi. WSW Alamos (50929); Alamos (50930); Guirocoba (50931-51).

Individuals of this species were commonly found on tree trunks and branches, on rocks and other elevated places.

For the subspecific name of this form, we have followed Oliver (1943) rather than Mittleman (1941).

EUMECES CALLICEPHALUS Bocourt

Guirocoba (50735).

A single individual was collected and another seen at the lower edge of the oak belt. One was beneath a slab of oak bark on the ground, the other under a rock. No skinks were observed in the Tropical Deciduous Forest, nor were any brought to us by native collectors, who presumably collected largely in this habitat. It is possible that this lizard does not range below the oak belt.

E. callicephalus is known to the Mexicans at Guirocoba as *ajolote* and is feared by the women who believe it to enter the genital tract. This same name and story are applied to *Bipes biporus* in Baja California.

CNEMIDOPHORUS BURTI Taylor

San Carlos Bay, 10 mi. WNW Guaymas (54640).

Collected by Frank Berberich and Al Allanson, October 15, 1951. The color pattern is very close to the type as illustrated by Taylor (1936a), the chief difference being that the vertebral lines are distinct, not fused into a single broad line. Smith and Taylor's key (1950) refers to *C. burti* as 5-lined, whereas our specimen possesses six distinct light lines. This individual is an adult, snout-vent length 91 mm.

CNEMIDOPHORUS SACKI COMMUNIS Cope

Agua Marín, 8 mi. WSW Alamos (50714); 12.4 mi. NW Navajoa (50715-21), 50723); Guirocoba (50722, 50724-34).

Two adult males, snout-vent length 95 mm in each, from NW of Navajoa, show no trace of a lined pattern dorsally. The pattern consists of numerous well-defined spots which were, in life, bright yellow against a black background. The head and nape were uniform gray-brown. Lizards from this locality differ from *C. sacki stictogrammus* in the wider spacing of the paravertebral lines of the juveniles and in ventral black coloring in two adult males.

Adults from Guirocoba, though larger than the Navajoa specimens, still retain the paravertebral stripes (faintly in some instances) and are generally much duller in coloration with less well defined spotting. The color of the venter is inconsistent, being black in some adult males and white in others.

Perhaps the Navajoa specimens are representatives of an unnamed race of the coastal plain Thorn Forest, contrasting with the lizards of the foothill Tropical Deciduous Forest at Alamos and Guirocoba.

CNEMIDOPHORUS TIGRIS AETHIOPS Cope

35.2 mi. S Hermosillo (50846-48).

This locality was a rather barren plain dotted with mesquite trees. In the sparse vegetation, the lizards could be observed at considerable distances as they foraged for food in the early morning. When a small rock was thrown near one of them, it would frequently mistake the bouncing rock for an article of food and attempt to run it down and eat it. The lizards often detected a moving stone at distances as great as 40 feet.

HELODERMA HORRIDUM (Wiegmann)

Guirocoba (50863-66).

One individual had eaten 13 birds eggs resembling in size (13x24 mm) and shape quail eggs. Another had taken a nestling bird *Piaya cayana*, squirrel cuckoo (identified by Dr. Frank Pitelka), which might have been dead when taken.

William Reeder found a large adult *Heloderma* active shortly after sunrise.

BOA CONSTRICTOR IMPERATOR Daudin

Guirocoba (50867-71); 49 mi. N Hermosillo (37799).

Seven boas were obtained at Guirocoba, two of which are alive at this writing (Nov. 1, 1952) and thus not in the list above. One collector said that they were most common amid the grass and low plants of valleys and rare or absent in hilly situations.

The individual from north of Hermosillo was taken just after it crossed a road on the morning of October 28, 1941, by Dr. S. B. Benson. The previous northern record had been Hermosillo (Allen, 1933).

LICHANURA ROSEOFUSCA GRACIA Klauber

Opposite Guaymas Airport (56515).

This individual, an adult, was collected April 27, 1952 by Sterling Bunnell. It is very similar to *Lichanura trivirgata* of Baja California.

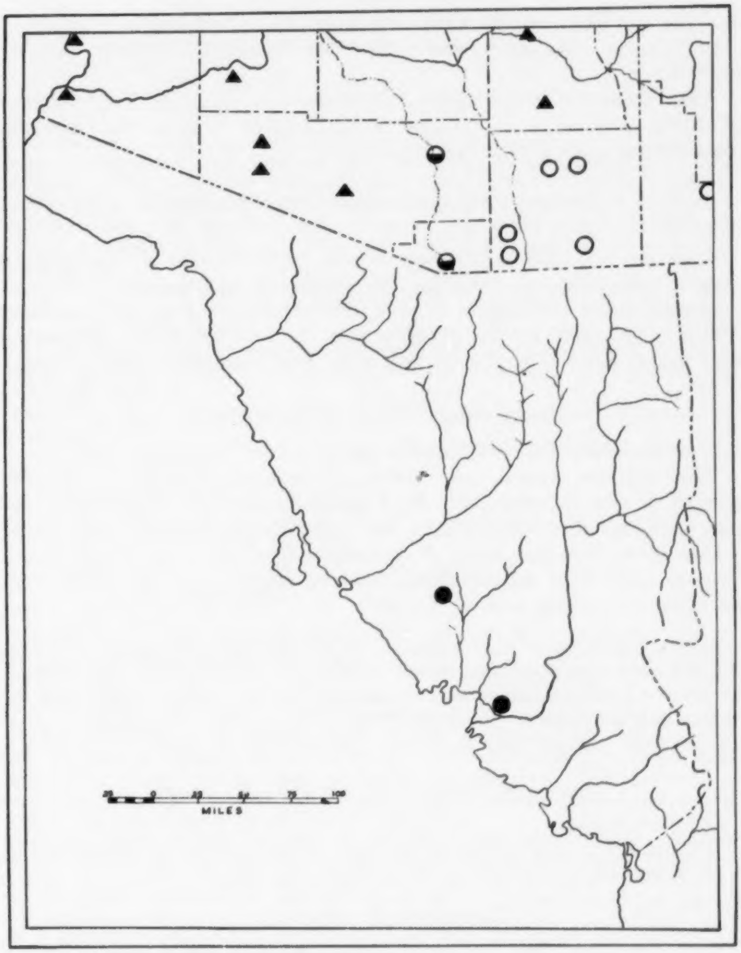

Fig. 1.—Distribution of *Lampropeltis getulus* in Sonora and adjacent Arizona and New Mexico. Triangle, *L. g. yumensis*; open circle, *L. g. splendida;* closed circle, *L. g. nigritus;* half-closed circle, three-way intergrade.

PHYLLORHYNCHUS BROWNI FORTITUS Bogert and Oliver

13.5 mi. W Alamos (50740); Guirocoba (SDSNH 18167).

The specimen from west of Alamos was found DOR in the Tropical Deciduous Forest. It is an adult male, snout-vent length 342 mm, tail length 58 mm, and has the following characters: dorsal scale formula 21-17-15; ventrals 155; subcaudals 34; supralabials 6/6; infralabials 9/9; anal entire. There are twelve dark blotches on the body and three on the tail. The Guirocoba specimen is a juvenile, s-v length 182 mm. These are the second and third specimens of this race to be reported.

THAMNOPHIS CYRTOPSIS CYRTOPSIS (Kennicott)

39.3 mi. N Hermosillo (50763); 26.2 mi. S Nogales (54641); Guirocoba (50754-62).

The Hermosillo and Nogales individuals were found on the road, one DOR, the other alive on the road in the daytime. One of the Guirocoba specimens had eaten a *Bufo mazatlanensis*.

THAMNOPHIS EQUES MEGALOPS (Kennicott)

26.8 mi. S Nogales (50764).

A single individual of this species was found beneath a rock under a mesquite tree 150 yards from the Rio Magdalena on August 3, 1950. At the same locality on August 21, a DOR of the same species, too badly crushed to be saved, was seen. This species has been listed from Sonora for many years, but we have been unable to find any other specific locality records.

DRYMARCHON CORAIS RUBIDUS Smith

Guirocoba (50801-08, 50810-12, 50872-77).

This was the second most commonly collected snake at Guirocoba, exceeded in our collection only by *Leptophis diplotropis*. *Drymarchon* appears to be a rather indiscriminate feeder. Specimens examined were found to have eaten *Bufo punctatus*, *B. mazatlanensis*, *Hyla baudini* and *Cnemidophorus sacki*. One individual was observed catching poeciliid fishes trapped in an evaporating pool in a canyon.

Individuals observed and collected by the authors were active by day. One was found at the lower margin of the oak forest among the roots of a cypress (*Taxodium mucronatum*) beside a stream. Others were seen by streams in the Tropical Deciduous Forest. *Drymarchon* was notably more common near streams than elsewhere.

LAMPROPELTIS DOLIATA NELSONI Blanchard

Guirocoba (50813).

This snake, a large adult female, was brought in by a Mexican who found it crossing a trail late in the evening of August 13th.

LAMPROPELTIS GETULUS

This species of king snake has not previously been reported from southern Sonora. This southern population represents a new subspecies.

Lampropeltis getulus nigritus subsp. nov.

Type.—No. 50814 in the collection of the Museum of Vertebrate Zoology, taken at 30.6 miles (by road) south of Hermosillo, Sonora, on the main highway on August 3, 1950 by Kenneth S. Norris and Richard G. Zweifel. One paratype, SNHM 12915, from 7.2 miles southeast of Pitahaya, Sonora, has been made available to us through the courtesy of Jay Savage. It was taken by John Figg-Hoblyn, Jay Savage and John Lamont on July 15, 1950.

Diagnosis.—Most closely related to *L. g. yumensis* and *L. g. splendida*, with which it intergrades. It differs from all other forms of *L. getulus* in its uniform dark brown or slaty black dorsal coloration without any trace of rings or stripes and in its high dorsal scale count.

Description of the type specimen.—Adult male, snout-vent length 915 mm, tail length 166 mm (after alcohol preservation). Scale row formula

$$25 \; \frac{5+6 \;\; (14)}{5+6 \;\; (13)} \; 23 \; \frac{-6 \;\; (140)}{-6 \;\; (146)} \; 21 \; \frac{4+5 \;\; (184)}{4+5 \;\; (184)} \; 19 \;\; (219)$$

The method of presenting scale row reduction is that of Dowling (1951). In all instances in which dorsal scale counts are given, the first count was taken on the neck at a distance back of the angle of the mouth equal to the distance from the angle of the mouth to the tip of the snout. Rostral single; internasals 2; frontal shield-shaped, somewhat longer than high; preoculars 1/1; postoculars 2/2; supralabials 7/7; infralabials 9/9; first temporal rows 3/3, t_2 3/3, t_3 5/3; ventrals 219; caudals in two rows of 56; anal single.

Color in alcohol.—Head scales all slate black except for anteroventral whitish mark on rostral. Anterior pair of chin-shields with yellowish-white centers. Dorsal body scales all slate black. Lateral body scales black with very dark brown centers, extending dorsally 4 or 5 scale rows from ventral scales. Ventral scales on anterior 1/3 of body occasionally flecked with irregular whitish-yellow blotches. Posterior 2/3 of ventrals and caudals black (Plate 1).

Description of paratype.—With only two specimens available, statistical comparisons are not possible.

Adult female, snout-vent length 795 mm, tail length 107 mm (after preservation). Dorsal scale formula

$$27 \; \frac{5+6 \;\; (8)}{6+7 \;\; (8)} \; 25 \; \frac{4+5 \;\; (23)}{4+5 \;\; (23)} \; 23 \; \frac{+6 \;\; (29)}{+7 \;\; (35)} \; 25 \; \frac{5+6 \;\; (122)}{5+6 \;\; (119)}$$

$$23 \; \frac{-6 \;\; (158)}{-6 \;\; (159)} \; 21 \; \frac{4+5 \;\; (209)}{4+5 \;\; (209)} \; 19 \;\; (217)$$

Rostral single; internasals 2; frontal shield-shaped; loreal nearly square, somewhat longer than high; preoculars 1/1; postoculars 2/2; supralabials 7/7; infralabials 10/10; first temporal rows 2/2; t_2 3/4; t_3 5/5; ventrals 217; caudals in two rows of 48; anal single.

Color in alcohol.—Head scales all dark chocolate brown except whitish ventral margin of rostral. Mental, infralabials and supralabials centered with lighter brown vertical markings. Chin-shields with irregular small whitish punctuations and lighter brown areas. Body scales all brown with dark brown margins. Slight tendency for lateral body scales and caudal scales to have more contrast between centers and edges. About ½ of ventral scutes irregularly blotched with white, size and occurrence of blotches decreasing posteriorly. Caudals with dark brown centers (Plate 1).

The loreal scales of both the type and paratype are somewhat longer than high, as in *L. g. yumensis* (occasional in *L. g. splendida*). Ventral scale counts (type 219, paratype 217) fall near the average of the range of variation for *L. g. splendida* (207-225; average 216) and near the lower limit given for *L. g. yumensis* (219-240, average 230) (Blanchard, 1921).

Intergradation.—The characteristics of the type and paratype suggests that *nigritus* possesses genetic materials of both *splendida* and *yumensis*. The shape of the loreal suggests relationship to *yumensis*, while ventral counts are suggestive of *splendida*. The presence of brown centers in dark brown lateral body scales is possibly indicative of a relationship to the speckled condition of *splendida*.

Two specimens have been examined from 5 miles north of Nogales, Santa Cruz County, Arizona. This locality is directly between known populations of *yumensis* to the west and *splendida* to the east. These specimens are of particular interest as they seem to be intermediate between *splendida, yumensis* and *nigritus* in several respects.

An adult male (s-v length 1012 mm) collected by C. H. Lowe, Jr. (AMNH 64819) is of particular interest. This animal has only the slightest trace of dorsal rings and appears unicolor above to all but the closest examination. Anteriorly, the dorsal body color is a very dark chocolate brown, lightening somewhat posteriorly to a dark rusty brown (in alcohol). Dorsal body scales are lightest in their centers showing a tendency toward the speckled condition typical of *L. g. splendida*. This tendency is further demonstrated by the presence of yellowish cream spots in the centers and edges of many body scales in the first two lateral rows. About ¼ of the anterior ventral scutes are

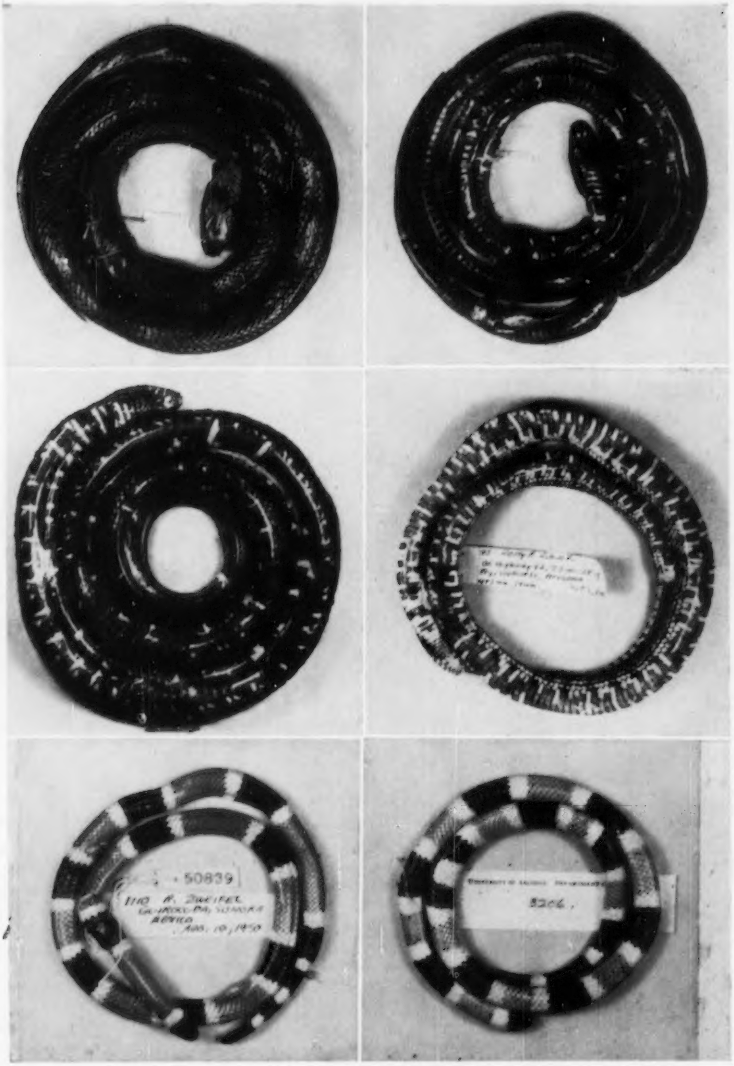

Plate 1.—Upper left, *L. g. nigritus*, type, MVZ 50814. Upper right, same, ventral surface. Center left, intergrade between *L. g. nigritus*, *L. g. splendida* and *L. g. yumensis*, ventral surface, AMNH 64819, 5 mi. N Nogales, Santa Cruz County, Arizona. Center right, ventral surface, *L. g. splendida*, MVZ 44747, 7.5 mi. SE Fry, Cochise County, Arizona. Lower left, *Micruroides euryxanthus australis*, type, MVZ 50839, Guirocoba, Sonora. Lower right, *M. e. euryxanthus*, UA 3206, Tucson, Pima County, Arizona.

irregularly blotched with yellow cream. This blotching decreases caudad; caudal scales are solid black. This represents a condition intermediate between the relatively dark

venters of the type and paratype of *nigritus* and the condition of *splendida* and *yumensis* (Plate 1). Dorsal scale formula

$$23\ \frac{5+6\ \ (10)}{5+6\ \ (14)}\ 21\ \frac{-6\ \ (38)}{-6\ \ (38)}\ 23\ \frac{-5\ \ (135)}{-6\ \ (137)}\ 21\ \frac{4+5\ \ (174)}{4+5\ \ (177)}\ 19\ \ (220)$$

This count is lower in the neck region than either of the specimens of *nigritus*, but within the limits of *yumensis* and *splendida*.

The other intergrade (MVZ 38591) is an adult female, s-v length 580 mm. The lateral body scales of this animal are dark blackish-brown with yellowish-white central punctations extending dorsally six rows on the anterior one third of the body, five rows at mid-body and four rows over the cloaca. The spotting extends to the tip of the tail. The spots are larger anteriorly. Mid-dorsal body and tail scales are dark brown to black (in alcohol). There is no trace of rings evident in this specimen. Dorsal scale formula:

$$25\ \frac{5+6\ \ (10)}{5+6\ \ (9)}\ 23\ \frac{-6\ \ (142)}{-6\ \ (142)}\ 21\ \frac{4+5\ \ (197)}{4+5\ \ (193)}\ 19\ \ (213)$$

Mr. William Woodin III has noted (personal communication) that king snakes from the region of Tucson, Pima County, Arizona, are frequently quite dark, tending toward *L. g. nigritus* in this respect.

A marked tendency toward darkening of light body scales is present in *yumensis*. Blanchard (1921) says "Its [*yumensis*] pattern differs from that of *boylii* in that the white centers of the dark scales, derived from *splendida*, do not cover the whole of the scale, but are mainly limited to the distal portion. Northward this condition very soon changes into that of typical *boylii;* that is, the white spreads over all of the scale, producing rings of continuous white. Westward, however, the pattern of *yumensis* is retained. In the vicinity of Yuma the light rings are often heavily suffused with brown."

Probably the light scales of the body rings in *yumensis* are increasingly suffused with brown southward into Sonora until the condition typical of *nigritus* is reached, in which the light rings are completely obscured by brown or black.

This new subspecies is named *nigritus* (L.; blackened) because of the tendency toward darkening which it shows compared to adjacent subspecies.

The type was taken at 11:30 P.M. just as it crawled off the road toward a dense growth of plants growing in a roadside pond. The surrounding area was semidesert vegetated by mesquite trees (*Prosopis*), palo verdes (*Cercidium*) and tree morning glorys (*Ipomea arborescens*). The paratype was likewise collected alive on the road at night.

RHINOCHEILUS LECONTEI ANTONI Dugés

Guirocoba (50738-9; SDSNH 18163).

Bogert and Oliver (1945: 370) have figured an individual of this race from Guirocoba in which the interspaces between the black rings are largely red. One of our Guirocoba specimens was similar, but the other had, in life, only a slight pink suffusion laterally in the light interspaces. This individual was predominately black and white.

SDSNH 18163 has dark rings which in most instances fuse with one another laterally, restricting the light interspaces to circular blotches. The areas of light scales located laterally in the dark rings tend to fuse with one another to form a continuous lateral light line.

RHINOCHEILUS LECONTEI CLARUS Klauber

20.4 mi. N Hermosillo (50737).

This individual was found alive on the road on the evening of August third. Dr. L. M. Klauber, who kindly examined the specimen, expressed the opinion that the snake should be referred to *clarus* but noted that it showed some tendency towards *antoni*. It differs from typical *clarus* in possessing (in life) red in the interspaces between the dark dorsal blotches.

Rhinocheilus lecontei lecontei

Sonoyta (LMK 38659).

Rhinocheilus l. lecontei × Rhinocheilus l. clarus

3 mi. S. Sonoyta (LMK 40031).

LMK 40031 is intermediate between *lecontei* and *clarus*.

Masticophis flagellum piceus

Guirocoba (50881); 12.4 mi. NW Navajoa (50879-80); 47 mi. (by road) N Guaymas (50878); 11.4 mi. N Hermosillo (50883); 37.1 mi. S Santa Ana (50882); 19.4 mi. S Santa Ana (50884).

These racers exhibit considerable variation in coloration. The most northerly adult specimen (37.1 mi. S Santa Ana) is entirely black dorsally except for the tip of the tail. Snakes from 11.4 mi. N Hermosillo and 47 mi. N Guaymas are black on the anterior third of the body, the color gradually changing to tan on the posterior portion. Perhaps the variation within the black phase is ontogenetic. Two large adults from near Navajoa are light tan. The Guirocoba specimen is reddish-brown, and is an adult.

When first observed on August 5, 1950, the Navajoa specimens were mating. They were twined about one another two feet off the ground in a dense, spiny bush. The female contained ova 25 mm in length.

The Guirocoba specimen had eaten a *Sceloporus clarki.*

Masticophis bilineatus bilineatus Jan

Guirocoba (50793-96).

The subspecific allocation of these specimens is somewhat uncertain. They resemble *M. b. lineatulus* Hensley in the possession of a narrow dorsolateral line and spotted gular area, but are like the typical form in that the dorsolateral light lines commence about four scales posterior to the last supralabial. They also agree with *M. b. bilineatus* in having a relatively light dorsal ground color.

Following Hensley's (1950) outline of the ranges of these two forms, we allocate these specimens to *M. b. bilineatus* but recognize that examination of larger numbers of specimens may alter the picture somewhat.

Masticophis striolatus striolatus Mertens

1 mi. NW Alamos (28289); Guirocoba (50797-800).

Bogert and Oliver (1945) have demonstrated that this form is specifically distinct from *M. flagellum,* showing differences in color pattern and scale counts. In addition to the differences noted by Bogert and Oliver, there are also proportional differences. *M. striolatus* possesses a wider head and heavier body. For example, three specimens of *M. striolatus* have a head width/length ratio of from 0.528 to 0.536, while seven Sonoran *M. flagellum* range from 0.429 to 0.489.

Salvadora hexalepis deserticola Schmidt

39.6 mi. S Santa Ana (50743); Guirocoba (50744); between Guaymas and Guaymas Airport (56520).

The Santa Ana specimen was DOR.

Leptophis diplotropis Günther

Guirocoba (50765-92); Mirasol, 16 mi. NE Alamos (SDSNH 18176).

This was the most abundant snake in the Guirocoba collections, being

represented by 28 specimens. One was found pursuing an *Agalychnis* along the base of a rock wall near a stream; another was found threaded through the top of a four foot bush. Both were collected in the daytime.

Contrary to the behavior of individuals of this species encountered by Oliver in Oaxaca (Oliver, 1948), the Guirocoba snakes proved to be extremely vicious, biting and deliberately chewing whenever the opportunity offered. Oliver has mentioned the possibility that these snakes possess a venom of low virulence; our experience seems to confirm this. A bite by one of them is followed by a prolonged stinging sensation in the immediate vicinity of the bite. While not severe, the reaction is noticeably greater than would follow a bite by another snake of similar size and temperament, such as a racer. A slight but persistent inflammation also resulted.

Leptophis was found to have fed on *Pternohyla* and *Hyla baudini*.

GYALOPION DESERTORUM (Taylor)

6.1 mi. NW Navajoa (50741); Guirocoba (50742).

The Navajoa specimen was DOR in the Thorn Forest. Body blotches of the two specimens are respectively 30 and 31, tail blotches 7 and 9.

TANTILLA YAQUIA YAQUIA Smith

Mirasol, 16 mi. SE Alamos (SDSNH 18190).

Hartweg (1944) described *T. bogerti* from Acaponeta, Nayarít, and noted its close affinity to *T. yaquia*. A distance of about 400 miles separates the type locality of *T. yaquia* (Guasaremos, Chihuahua) from that of *T. bogerti*. The present (Mirasol, Sonora) specimen was taken about 70 miles south of Guasaremos.

The Mirasol specimen shares characters with both *yaquia* and *bogerti*. It resembles *bogerti* in that the first pair of infralabials meet on the midline, separating the mental from the anterior chinshields, and in that the third and fourth (rather than the fourth and fifth) supralabials enter the orbit. It resembles *yaquia* in that the black head cap extends only 2¼ scales back of the parietals along the mid-line (fig 2).

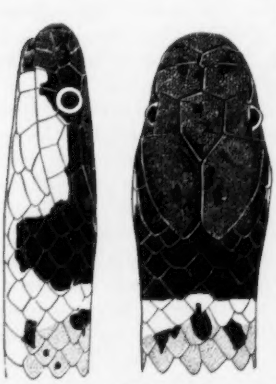

Fig. 2.—Head scalation and pattern of *Tantilla yaquia yaquia*, SDSNH 18190, Mirasol, Sonora.

The only male specimen of *T. bogerti* has 140 ventrals (Hartweg, 1944), the Mirasol specimen 144 ventrals. According to Hartweg, the differences in number of subcaudals, 66 in the female type of *yaquia* and 46 in the only female specimen of *bogerti*, are of greatest importance in separating the two forms. The Mirasol specimen, a male, has an incomplete caudal series.

Since the Mirasol specimen exhibits characters of both *yaquia* and *bogerti*, and since differences in scalation are subject to clinal variation in many snakes occurring along the west coast of Mexico, we prefer to consider the two as sub-specifically related. The Mirasol specimen is referred to *T. y. yaquia* largely on the basis of its geographical location.

CHIONACTIS PALAROSTRIS PALAROSTRIS (Klauber)

40.7 mi. S Hermosillo (50808).

This specimen has been reported by Klauber (1951). It was found DOR in a region where the surrounding desert was characterized by scattered mesquite and palo verde trees on rather bare soil.

SONORA AEMULA (Cope)

Guirocoba (50746, SDSNH 18169, LMK 41107).

This species is now known from a total of five specimens, all from Guirocoba except the type, which is from Batopilas, Chihuahua, and a cast skin from Alamos, Sonora.

The body color pattern is variable. In all specimens, each red scale is centered with black, but the arrangement of the red, black and white rings shows little consistency. The smallest specimen (MVZ 50746, female, s-v length 172 mm) is reddish anteriorly with two white rings on the posterior portion of the body and one on the tip of the tail. Each of these white rings is bordered by a pair of black rings, and pairs of black rings bordering adjacent white rings are separated by wide red areas. The pattern is similar to that described by Bogert and Oliver (1945) for their Guirocoba specimen (s-v length 200 mm).

The largest individual (LMK 41107, female, s-v length 336 mm) has red, black, and white rings all along the body and tail but in no definite order. Of the six red rings, four are bordered by black on both sides and two by black on one edge and white on the other. In SDSNH 18169 (s-v length 250 mm male), the rings occur in a definite pattern. Beginning with a red ring following the nuchal black ring, the pattern is red-white-black-white, red-white-black-white so that in this individual all the red rings except the first are bordered on each side by white rings. Furthermore, the rings are narrower and more numerous than in LMK 41107.

All specimens, both male and female, possess the strongly keeled caudal scales which have led to the reference of this form to a montotypic genus, *Procinura*. We agree with Bogert and Oliver (1945) that this species is sufficiently close to other members of the genus *Sonora* that separation into a monotypic genus would serve only to obscure its relationships.

LMK 41107 contained seven eggs each measuring about 13.0 x 16.5 mm. Unfortunately the exact date of collection for this individual, which was taken in the spring, is not available.

LEPTODEIRA EPHIPPIATA Smith and Tanner

Guirocoba (50835-6); 7 mi. SE Alamos (LMK 41181).

These three specimens constitute the third, fourth and fifth individuals of the species to be reported. As might be expected, they add slightly to our knowledge of the range of variation within the species. The male specimen (50836) has 175 ventrals and 87 subcaudals; the females have 185 and 188 ventrals and incomplete caudal series. Two of the snakes differ from the type in that the postocular dark stripe is continuous with the nuchal blotch, while in the other continuity is not quite established.

One of the specimens was found under a pile of flood-washed plant debris in a canyon at Guirocoba, a situation also frequented by *Leptodactylus* and *Rana pipiens* which probably serve as food for the snake.

HYPSIGLENA TORQUATA OCHRORHYNCHA Cope

Ensenada del Perro, S end Tiburon Island (37802); Guirocoba (50830-32); 44 mi. S Hermosillo (50829).

The Tiburon Island specimen was collected November 10, 1941 by Charles Sibley. *Hypsiglena* does not seem to have been previously reported from this island. Of the mainland specimens, the Guirocoba individuals are considerably darker in dorsal ground color than the specimens from the more arid areas to the north. Our specimens show none of the typical *torquata* nape pattern. Pending further study, we do not follow Langebartel and Smith (1954) in the use of the name *H. ochrorhyncha chlorophaea* for the Sonoran population of this species.

OXYBELIS AENEUS AURATUS (Bell)

20 mi. NE Hermosillo (26161); Bahia San Carlos (51642); Guirocoba (50815-28); Mirasol, 16 mi. SE Alamos (SDSNH 18189).

At Guirocoba this was the third most abundantly obtained snake, being exceeded in number only by *Leptophis* and *Drymarchon*. One individual was encountered crawling rapidly along the ground with its head well elevated above the surface.

The lack of sharp distinction between the dorsal and ventral coloration may be related to the presumed semiarboreal habits of the animal. The grayish ground color of *Oxybelis* is strikingly similar to the color of certain climbing vines abundant at Guirocoba.

At Guirocoba, *Oxybelis* was the object of the milksnake myth. We were assured that the snake would suck the milk from cows, leaving the udder hard and dry.

TRIMORPHODON LAMBDA Cope

San Carlos Bay, 10 mi. NW Guaymas (54642).

This individual was collected on October 16, 1951 by John Fleet. With its V-shaped pattern on the posterior portion of the head and narrow dorsal blotches, 30 in number, it is quite different from the Guirocoba specimens of *T. upsilon*.

TRIMORPHODON UPSILON Cope

Guirocoba (50833-34), SDSNH (18178).

These three specimens constitute the first record of this species for the state of Sonora, although it has been reported from Batopilas, Chihuahua, which is 60 miles east of Guirocoba (Cope, 1879). These specimens have fewer (19, 20, 22) body blotches than the minimum of 23 previously reported by Smith (1941) for this species, and thereby fit into the east to west clinal reduction in number of body blotches which he noted.

MICRURUS DIASTEMA DISTANS (Kennicott)

Guirocoba (50837).

This specimen was obtained by purchase and was brought in alive. It was extremely active and characteristically struck from side to side to bite a stick when touched with it. This behavior contrasted with the normally lethargic attitude of *Micruroides*. After being annoyed for some time, the *Micrurus* hid its head beneath its body and coiled up the tip of its tail. The tail was then held above the body and moved about in a manner

strikingly reminiscent of the actions of the head, not unlike the similar habit of *Diadophis.*

MICRUROIDES EURYXANTHUS (Kennicott)

Specimens of this species obtained at Guirocoba appear to differ sufficiently from those to the north to deserve subspecific recognition.

Micruroides euryxanthus australis subsp. nov.

Type.—Adult male, Museum of Vertebrate Zoology No. 50839, obtained August 10, 1950, by Richard G. Zweifel and K. S. Norris by purchase from a native collector at Guirocoba, Sonora, Mexico. Snout-vent length 377 mm, tail length 33 mm (in alcohol). Dorsal scales in 15 rows; 226 ventrals; 25 subcaudals. Ten black, 10 red and 21 white rings on the body, 3 black, 2 white and no red on tail.

Paratypes.—Four specimens have been available which may be considered paratypes. These are MVZ 50838 and 50840 and AMNH 63742, all three from Guirocoba, and AMNH 64249 from Alamos.

Diagnosis.—*Australis* differs from typical (northern) *euryxanthus* in having wider red rings. This character is best expressed by counting the number of red scales along the mid-line of the body, excluding any red on the tail. Five specimens of *M. e. australis* have from 100-107 red scales, mean 104.4 ± 1.6. The same counts for 56 *Micruroides* from Arizona and New Mexico yield a range of 42-93 red scales, mean 72.2 ± 1.4. In the five specimens of *australis,* the red rings are immaculate. *M. e. euryxanthus* frequently has black markings in the red rings, occasionally obliterating the red almost entirely. However, this character is not sufficiently consistent to be useful in a key.

Other than the type and paratypes of *australis,* only six Sonoran specimens have been available to us. One of these, UIMNH 5651 from extreme northern Sonora (8.6 mi. S Sonoyta), has rather wide red rings, a total of 93 red scales along the midline, but these red rings are in part contaminated with black, unlike typical *australis.* AMNH 3909 from Las Chispas, lies within the range of *euryxanthus,* having 83 red scales. We have been unable to find this locality on any map. USNM 1122 and 1131, the former being the type of the species, have 83 and 96 red scales respectively. Dr. Doris M. Cochran kindly furnished the data on the type. Both of these specimens bear as their only locality data "Sonora, Mexico." Smith and Taylor (1950), without presenting evidence for the proposition, have restricted the type locality of *M. euryxanthus* to Guaymas. A single specimen from Tiburon Island (USNM 9566) has 88 red scales on the mid-line. MVZ 56522 from 30 mi. N Hermosillo, has 95 red scales along the middorsal line and is the only intermediate specimen with adequate locality data. There are as yet insufficient specimens to define the extent of the area of intergradation.

USNM 8566 from Chihuahua, is typical *M. e. euryxanthus* and probably came from the northwestern corner of the state. The record of *Micruroides* from Batopilas, Chihuahua (Cope, loc. cit.) probably refers to *M. e. australis,* inasmuch as Batopilas is only about 60 miles from Guirocoba.

TABLE 1.—Characters of pattern and scutellation of *Micruroides euryxanthus*

		M. e. euryxanthus (Arizona and New Mexico)	*M. e. australis* (Southern Sonora)
Ventral scales	♂	223.37 ± 0.96(214-233)n=32	221.3(217-226)n=3
	♀	233.06 ± 1.34(225-244)n=16	226.0(225-227)n=2
Subcaudal scales	♂	26.75 ± 0.78(23- 29)n=32	25.6(25- 26)n=3
	♀	24.06 ± 0.39(22- 27)n=16	24.5(23- 26)n=2
Dorsal red scales		72.19 ± 1.43(42- 93)n=56	104.4 ± 1.6(100-107)n=5
Body black rings		11.54 ± 0.12(10- 13)n=57	11.0 ± 0.6(10- 13)n=5

Variation in scalation and pattern is summarized in Table 1 for material from Arizona, New Mexico and southern Arizona. Notable is the extensive sexual dimorphism in ventral scales. The Tiburon Island specimen (USNM 8566) is unique in that it, a male, possesses 250 ventrals, 6 more than the greatest number recorded for even any

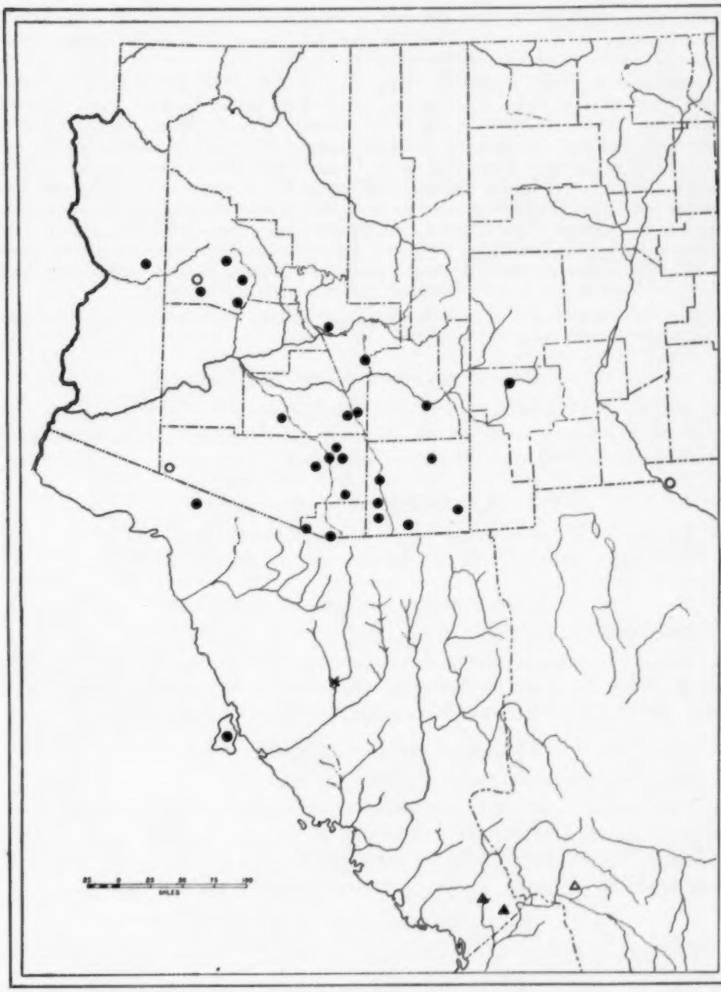

Fig. 3.—Distribution of *Micruroides euryxanthus*. Dot, *M. e. euryxanthus;* triangle, *M. e. australis;* cross, intergrade. Closed symbols indicate one or more specimens examined, open symbols are literature records.

mainland female. If one were inclined to recognize races on the basis of ventral counts alone and if future specimens prove to have similarly large numbers of ventrals, the island population could receive nomenclatural recognition.

Distribution.—*M. e. australis* is known to us from specimens only from extreme southeastern Sonora. The specimen reported by Cope (1879:263) from Batopilas, Chihuahua, is presumably of this subspecies. *Specimens examined:* Guirocoba (4); Alamos (1).

M. e. euryxanthus ranges from central Arizona, approximately the edge of the plateau region, south and east to include southwestern New Mexico, extreme western

Texas (Brown, 1950:209), northwestern Chihuahua and northern Sonora, including Tiburon Island. To the west, the range does not seem to include the extreme western edge of Arizona nor extreme northwestern Sonora (fig. 3).

Specimens examined: ARIZONA: PIMA Co.—Tucson (12), also 4 mi. N, 10 mi. N, 5 mi. N, 6 mi. NE, 9 mi. E, 10 mi. E, 18 mi. SW; mouth Sabino Canyon; Roosevelt; Santa Rita Mountains; Santa Catalina Mountains; 5 mi. S Oracle Junction. COCHISE Co.—Fry; Highway 82, 6 mi. E junction highways 82-92; 2 mi. NNE Dos Cabezos; 1 mi. SE Dos Cabezos; 2 mi. E Benson; 30 mi. NE Douglas; Fort Huachuca; Bisbee. SANTA CRUZ Co.—Nogales; Warsaw Mill; near Ruby. YAVAPAI Co.—Congress Junction; 6 mi. NE Castle Hot Springs; Fort Whipple; Cleator (2). GRAHAM Co.—Solomonville. PINAL Co.—Santa Cruz Village; Tiger; near Mammoth. GILA Co.—Roosevelt Reservoir; San Carlos. MOHAVE Co.—Signal. NEW MEXICO: GRANT Co.—11 mi. NE Cliff. SONORA: Sonora; Las Chispas; 8.6 mi. S Sonoyta; Tiburon Island; 30 mi. N Hermosillo (*australis* intergrade). CHIHUAHUA: Chihuahua.

We have named this race *australis* (L., southern) with reference to its southern position in the distribution of the species.

CROTALUS ATROX Baird and Girard

20.9 mi. N Hermosillo (50843); 27.7 mi. N Hermosillo (50844).

Both individuals were found crawling on the road in the evening, one on August 3, 1950, the other on August 20.

CROTALUS TIGRIS Kennicott

12.3 mi. N Hermosillo (50811); 11.5 mi. N Hermosillo (50842).

Both were found DOR on the evening of August 3, 1950.

KINOSTERNON SONORIENSE Le Conte

Rio Magdalena, 1 mi. SE Caborca (51355).

This specimen was obtained in the course of seining for fish on February 9, 1950. It agrees in pertinent characters with four individuals of the same species from the Penna Blanca Springs region of Arizona.

KINOSTERNON INTEGRUM Le Conte

Guirocoba (50889-902); Alamos (50907-10).

This is the most abundant turtle at Guirocoba. They were found even in small canyons where the water was at times restricted to disconnected potholes. The Alamos specimens were given to us by Mr. John Hilton and were probably collected in the immediate vicinity of that town.

PSEUDEMYS SCRIPTA HILTONI Carr

Guirocoba (50911); Arroyo Cuchujáqui, 8 mi. SE Alamos (UCLA 4777); Rio Yaqui, 20 mi. upstream from Cocorit (55384).

The Arroyo Cuchujáqui specimen, a large adult, was captured on February 5, 1950, when it attempted to hide under a rock in shallow water. Other individuals were present in a nearby deep pool in the stream.

The Rio Yaqui specimen represents a range extension of 100 miles to the northwest. More significant, perhaps, is that the record extends the known range of the genus two major drainage systems to the north, into a river draining much of north-central Sonora and which extends northward to the Arizona-Sonora border. This specimen, along with two other *Pseudemys* which escaped, was seined from a small, stagnant backwater area with a bottom of very soft mud. It was taken with eleotrid gobies, catfish and poeciliids.

GEOEMYDA PULCHERRIMA PULCHERRIMA (Gray)

Guirocoba (50912-13).

Both specimens were brought in after rains.

MEXICAN NAMES FOR AMPHIBIANS AND REPTILES

Bufo sp., sapo; *Leptodactylus*, ranita; *Agalychnis dacnicolor*, rana verde; *Phyllodactylus*, salamanquesa; *Anolis*, *Urosaurus*, cachorrita; *Ctenosaura*, iguana; *Holbrookia*, *Callisaurus*, perrito; *Phrynosoma*, camaleón; *Sceloporus*, cachorra, cachorrón; *Eumeces*, ajolote; *Cnemidophorus*, huico; *Heloderma*, escorpion; *Boa*, ilimacoa; *Drymarchon*, culebra prieta; *Lampropeltis doliata*, *Sonora aemula*, *Micrurus*, *Micruroides*, corál; *Leptophis*, culebra verde; *Leptodeira*, *Hypsiglena*, *Trimorphodon*, vibora sorda, viborita. *Oxybelis*, culebra virote; *Crotalus*, vibora de cascabel; *Geoemyda*, tortuga colorada.

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Notes and Discussion

Riccia Canaliculata Hoff. in Arkansas

The *Riccia fluitans* complex has long been recognized as presenting some interesting problems taxonomically. Recently the author collected this species in Arkansas as well as in Mexico and has compared notes on the two sets of collections offered here.

In the past, it has been customary to speak of broad and narrow forms, but with the study of chromosome numbers and critical morphological studies of cultures, there have resulted several species which the complex now contains. The aquatic form of each species is much narrower and less robust than the land form. This character alone is very useful in the field, for, *R. canaliculata* as the land form of this species is extremely thick for its width.

Carter (1935) worked with two collections of the group, made in California, grew them in culture and found she had a narrow and a broad form. It is clear from her drawings and photographs that she probably was working with two species of the complex. She stated that the narrow form came close to *R. canaliculata* and the broad form to *R. huebeneriana*. This *R. huebeneriana* mentioned is the one described by Underwood (1894), not the *R. huebeneriana* of Lindenberg (1836) and is now a synonym of *R. sullivantii* Aust. The broad form of her cultures were consistently sterile. The author's reaction to the first land form rosettes of *R. rhenana*, observed at Grassy Lake, Hempstead County, Arkansas was a field determination of *R. sullivantii*.

Carter goes on to say "The narrow thalli on soil cultures are slender and comparatively thick, have long, acute dichotomies and tend to spread out on the substratum rather than to form a definite rosette." Collections made in Arkansas compared favorably with these observations of the species in culture.

From an historical point of view, probably the earliest illustration of fruiting in *R. canaliculata*, was made by W. Wilson from collections in Cheshire, England in September, 1834. W. J. Hooker's column on "Botanical Information" in *The Companion to the Botanical Magazine* for 1835 comments on the collection and published the illustration under the name of *Riccia fluitans*, opposite page 193. This illustration as a whole, presents a problem as to what exact species of the complex it offers, due to the fact that no good, detailed cross-section of the thallus appears on the plate.

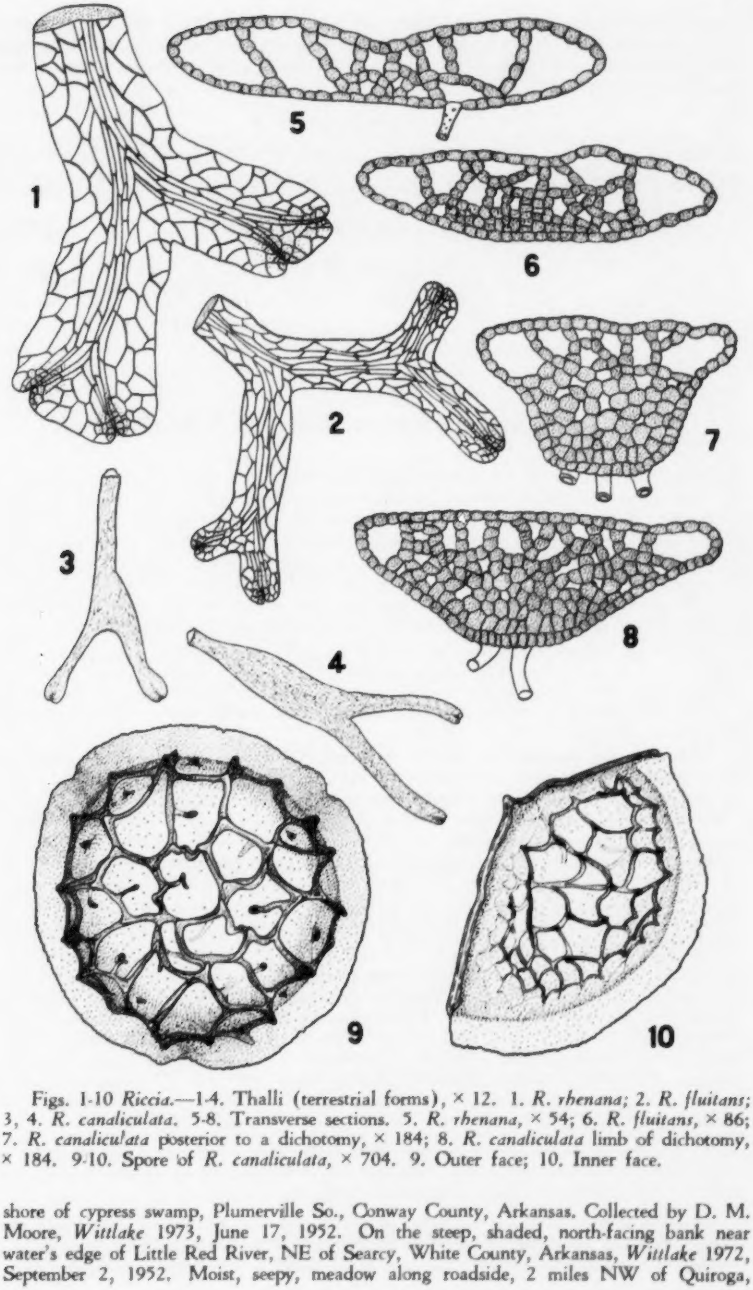
A small number of collections have been made in the areas designated above, and perhaps the differences observed in this paper on *R. canaliculata* will in time have greater or lesser significance. The author only wishes to present differences in the material at hand, compared with *R. canaliculata* material that coincides with Müller's (1941) description of the species, more closely.

The Arkansas material showed differences in the number of areolae across the outer face, (fig. 9); the number being usually greater than 3 to 4. The spore diameter ranged from 62 to 70 microns, definitely less than cited by Müller in 1941. The land form has both attenuated apices and spoon-shaped or spatulate apices at the end of dichotomies of the thallus, (figs. 3 and 4). The angle between dichotomies of the attenuated form is acute, between broad-tipped dichotomies, concave or rounded. The thallus form in fig. 3 was consistently thinner in transverse section than that illustrated in fig. 4. Transverse sections of both types of thalli were rather consistent in the general disposition of air chambers and parenchymatous tissue. In this respect, they coincide almost exactly to the transverse sections illustrated by Müller (1941).

The specimens collected in Mexico were all terrestrial forms and were growing near and around large boulders in a moist meadow northwest of Quiroga, Michoacan, and on the perpendicular walls, several inches above the water's edge of deep pools west of Ciudad Hidalgo in the same state. Compared to the Arkansas material, these collections differed in some respects as to spore characteristics and thallus structure.

In conclusion, the author wishes to express his appreciation to Dr. Roland L. McGregor of the Botany Department, University of Kansas for the identification of material and the many discussions concerning these taxa. The accompanying plate figures the land forms of *R. rhenana, R. fluitans* and *R. canaliculata* at the same magnification (figs. 1, 2, 3 and 4).

The following collections were referred to above: *Riccia canaliculata* Hoff. On the



Figs. 1-10 *Riccia.*—1-4. Thalli (terrestrial forms), × 12. 1. *R. rhenana;* 2. *R. fluitans;* 3, 4. *R. canaliculata.* 5-8. Transverse sections. 5. *R. rhenana,* × 54; 6. *R. fluitans,* × 86; 7. *R. canaliculata* posterior to a dichotomy, × 184; 8. *R. canaliculata* limb of dichotomy, × 184. 9-10. Spore of *R. canaliculata,* × 704. 9. Outer face; 10. Inner face.

shore of cypress swamp, Plumerville So., Conway County, Arkansas. Collected by D. M. Moore, *Wittlake* 1973, June 17, 1952. On the steep, shaded, north-facing bank near water's edge of Little Red River, NE of Searcy, White County, Arkansas, *Wittlake* 1972, September 2, 1952. Moist, seepy, meadow along roadside, 2 miles NW of Quiroga,

along Lake Patzcuaro, Michoacan, Mexico, *Wittlake* 1978, July 17, 1953. Around small pools near irrigation ditches in a rice-growing region, 4 miles west of Ciudad Hidalgo, Michoacan, Mexico, *Wittlake* 1977, July 16, 1953. E. B. WITTLAKE, Iowa State Teachers College, Cedar Falls.

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The Occurrence of the Parasite Sarcocystis in Mexican Birds

Avian host records of the cyst-forming genus *Sarcocystis* (until recently believed to be a protozoan but now considered by many to be a fungus; Spindler and Zimmerman, J. Parasit., Suppl. 31:13. 1945) were summarized by Erickson (Auk 57:514-519. 1940). It has been reported in 22 species of birds belonging to 13 families. Apparently there is only one avian host record from Central America—a falcon, *Leucopternis* sp., from Panama (Darling, J. Parasit. 1:114. 1915; also Erickson, *op. cit.*: 519). The following records from southern Mexico include four new host species for *Sarcocystis* and the first records of its occurrence in birds of the families Furnariidae and Troglodytidae.

At Pie de la Cuesta, Guerrero, on August 27, 1952, I collected an adult male rufous-naped cactus wren (*Campylorhynchus rufinucha humilis*) which had numerous cylindrical, white cysts in the muscles of the neck, breast, and legs (see Erickson, *op. cit.*, for description and illustrations of cysts). The neck was preserved and the cysts later were identified as those of *Sarcocystis* sp.

Following the discovery of the infected wren, all birds collected, wrens and others, were examined for presence of sarcocysts in the course of their preparation as study skins or skeletons. Although these examinations were rather superficial, being largely limited to gross inspection of the exposed surfaces of the skeletal muscles, it is doubtful whether a reasonably heavy, macroscopically visible infection could have escaped attention. No additional cases of infection were noted in 1952. During two subsequent collecting trips in southern Mexico, one October-November, 1953, and another March-June, 1954, more than 800 specimens of birds, the majority of which were wrens of the genus *Campylorhynchus*, were examined and several additional cases of infection were noted. These and the 1952 record are presented in table I.

The following data pertain to the infected birds, all of which were adult: *Synallaxis erythrothorax furtiva*, 2 males, 3 miles southwest Cosamaloapan, Veracruz, May 23, 1954. *Campylorhynchus chiapensis*, 1 male, 1 sex?, vicinity of Tonalá, Chiapas, March 30 and April 14, 1954. *Campylorhynchus r. rufinucha*, 1 female, 12 miles south-southwest Boca del Río, Veracruz, May 22, 1954. *C. r. humilis*, 1 male, Pié de la Cuesta, Guerrero, August 27, 1952; 1 female, Tonalá, Chiapas, April 14, 1954. *C. r. nigricaudatus*, 1 male, 12.1 miles southeast Tonalá, Chiapas, April 2, 1954. *Saltator coerulescens richardsoni*, 1 male, 2.7 miles southeast Tonalá, Chiapas, March 27, 1954.

In addition to the specimens of birds listed in the table, more than 1000 specimens of other Mexican species of various families (mostly of the order Passeriformes) were examined for the presence of macroscopic sarocysts, with negative results.

Erickson (Auk 57:515. 1940) reported a 2.68 per cent infection of *Sarcocystis rileyi* in 279 ducks of 18 species examined in the Division of Economic Zoölogy, University of Minnesota, and a 6.97 per cent infection in 43 ducks of eight species autopsied by the

Minnesota Wildlife Disease Investigation. Erickson (*loc. cit.*) pointed out that "since a large proportion of the ducks that come in for examination are sick, diseased, or crippled, it is probable that the percentage of infection . . . is much greater than in the duck population as a whole." He concluded that "the frequency of occurrence of *Sarcocystis* in birds is not known."

Percentages of occurrence of 1.68 for *Campylorhynchus chiapensis* and 1.49 for *C. rufinucha* may, I believe, closely approximate the frequency of gross infection in these species' populations, since the individuals examined were collected at random and the sample sizes are large. The possibility that infected individuals of the species herein reported were in a weakened condition, and hence, were more readily collected than those uninfected, seems unlikely in view of the fact that I noted no abnormalities in the infected birds as regards general behavior and appearance, weight, or gonadal development. The high percentages of infection in *Synallaxis erythrothorax* and *Saltator coerulescens* are noteworthy, but larger samples are needed before conclusions may be drawn as to the frequency of infection in those species.

I am indebted to Dr. Arnold B. Erickson, Game Research Supervisor of the Minnesota Department of Conservation, and to Dr. F. D. Wallace, parasitologist at the University of Minnesota, for identification of material.—ROBERT K. SELANDER, Museum of Vertebrate Zoology, Berkeley.

TABLE I.—Occurrence of *Sarcocystis* in Mexican Birds

Avian host and locality	Number examined	Number infected	Per cent infected
Furnariidae			
Synallaxis erythrothorax (Chiapas and Veracruz)	3	2	66.6
Troglodytidae			
Campylorhynchus chiapensis (Tonalá, Chiapas)	119	2	1.68
Campylorhynchus rufinucha (total of 3 races)	268	4	1.49
C. r. rufinucha (central Veracruz)	38	1	2.63
C. r. humilis (Oaxaca and Chiapas)	127	2	1.57
C. r. nigricaudatus (Chiapas)	103	1	0.97
Fringillidae			
Saltator coerulescens (Guerrero and Chiapas)	7	1	14.3

Further Notes on the Food of Alberta Amphibians[1]

In a previous paper (Amer. Midl. Nat. 52:221-224, 1954) we have indicated the nature of food taken by three of the common Alberta amphibians—*Rana pipiens, Pseudacris nigrita,* and *Bufo hemiophrys.* Subsequent investigations have involved studies of 63 stomachs from four additional species—*Rana sylvatica, R. pretiosa, Bufo boreas,* and *Ambystoma tigrinum.* The results of the analysis of stomach contents are presented in table 1 where for each species we have indicated the number of stomachs containing the various groups of invertebrates and also the numbers of invertebrate specimens represented. All identifications were made by the junior author. Many of the stomachs contained small quantities of vegetation and sand in addition to the animal material mentioned.

RANA SYLVATICA

The 36 stomachs used in the investigation of this species came from adults and subadults obtained as follows: 4 from Nordegg collected July 22, 1952; 5 from Rock Lake of which 2 were procured on July 3, 1 on July 26 and 2 on August 1, 1952; 11 from Gorge Creek of which 5 were collected June 10 and 6 on June 17, 1953; 1 from Beaverhill Lake June 5; 2 from Vermilion June 11; 3 from Delburne July 27; 10 from Lousana July

[1] Study based on materials obtained during zoological surveys made in the years 1951-1953 by the senior author with support from the General Research Fund of the University of Alberta.

TABLE 1.—Stomach contents of 36 *Rana sylvatica*, 12 *R. pretiosa*, 9 *Bufo boreas* and 6 *Ambystoma tigrinium*.

	Rana sylvatica		Rana pretiosa		Bufo boreas		Ambystoma tigrinum	
	A[2]	B[3]	A	B	A	B	A	B
MOLLUSCA	21	45	7	27	....	....	1	1
ANNELIDA	1	4	1	1	....	....	....	....
ARTHROPODA	36	420	12	178	9	590	6	21
ARACHNOIDEA	26	66	9	19	4	13	1	1
Araneida	22	37	7	16	4	10	....	....
Phalangida	1	2	....	....	....	....	....	....
Acarina	6	26	2	2	....	....	1	1
CHILOPODA	1	1	....	....	2	3	....	....
DIPLOPODA	....	....	1	1	....	....	....	....
INSECTA	36	354	12	159	9	577	6	20
Collembola	2	2	....	....	....	....	....	....
Orthoptera	4	4	....	....	3	9	3	6
Plecoptera	1	1	1	1	....	....	....	....
Ephemeroptera	1	1	2	8	....	....	....	....
Odonata	4	6	2	4	1	1	....	....
Hemiptera	10	20	2	2	5	11	2	3
Homoptera	12	13	1	1	1	1	2	3
Neuroptera	....	....	2	3	....	....	....	....
Coleoptera	29	122	10	27	7	55	2	2
Trichoptera	5	7	3	3	....	....	....	....
Lepidoptera	5	6	8	9	3	8	1	1
Diptera	28	133	12	83	3	8	3	5
Hymenoptera	20	39	8	18	9	484	....	....

[2] Number of stomachs containing designated invertebrates.

[3] Number of invertebrate specimens.

27, 1953. The first three localities are in the eastern part of the Rocky Mountains while the remainder are in the parkland region of Alberta. Our studies indicate that the food habits of *Rana sylvatica* in these two areas are essentially the same.

The data indicate that wood frogs in these localities feed chiefly on arthropods and to a lesser extent on snails, slugs, and earthworms. The major part of the arthropod material consists of insects with spiders being of secondary importance. Among the wide variety of insects taken, beetles and flies appear to be most important as food items while hymenopterans stand next in this respect.

The notes which follow contain a detailed listing of the food material represented in the 36 stomachs.

MOLLUSCA—44 snails and 1 slug.

ANNELIDA—4 earthworms.

ARTHROPODA: ARACHNOIDEA—37 spiders including 3 *Epeira trifolium*, 2 harvestmen, 26 mites consisting of 1 oribatid, 1 tyroglyphid, 11 uropod, 13 gamasid types, and 1 centipede. INSECTA (354 specimens). Collembola—2 individuals; Orthoptera—2 small oediponine grasshoppers and 2 grouse locusts, *Tettix granulosus;* Plecoptera—single individual; Ephemeroptera—1 mayfly nymph; Odonata—1 adult damselfly and 5 dragonfly nymphs; Hemiptera—9 lygaeids (4 adults and 5 nymphs), 1 nabid (*Nabis ferus*), 4 saldids (3 *Salda bouchervillei*), 4 gerrids (*Gerris* sp.), 1 corixid, and 1 undetermined; Homoptera—1 cercopid, 6 cicadellids, 2 fulgorids (1 *Delphacodes* sp.), 1 psyllid, 2 aphids, and 1 coccid; Coleoptera—18 carabids (3 *Pterostichus* sp. and 1 larval *Calosoma* sp.), 2 larval and 1 adult dytiscids, 1 gyrinid, 3 hydrophylids, 4 silphids (2 larval *Necrophorus* sp. and 2 adult *Silpha bituberosa*), 15 staphylinids, 2 melyrids (*Collops bipunctatus*), 1 meloid, 6 elaterids (1 *Hemicrepidius memnonius*), 1 buprestid, 3 byrrhids, 1 nitidulid, 9 coccinellids (1 *Anisoclavia 12-maculata*), 10 scarabeids (*Aphodius* sp.), 1

cerambycid (*Pachyta lamed*), 8 curculionids (7 *Otiorhynchus sulcatus*), 34 undetermined larvae of which 7 were aquatic, 2 undetermined adults; Trichoptera—7 caddis fly adults; Lepidoptera—3 caterpillars, 2 cutworms, and 1 moth; Diptera—73 tipuloids (64 winter gnats, 2 *Nephrotoma altissima*, 2 larvae and 5 adults unidentified), 7 chironomids (4 larvae), 1 culicid, 1 cecidomyid, 7 mycetophilids (5 larvae and 1 *Sciara* sp.), 1 bibionid, 4 stratiomyids (3 larvae probably *Odontomyia* and 1 adult *Microchrysa polita*), 5 dolichopodids (2 *Dolichopus* sp.), 6 syrphids (4 larvae, 1 *Melanostoma* sp., 1 *Metasyrphus* sp.), 1 trupanaeid (*Eutreta* sp.), 4 sepsids, 2 ephydrids, 1 tetanocerid, 2 muscids, 9 larval metopiids, 9 undetermined adults of which 8 were acalyptrate; Hymenoptera—8 tenthredinid larvae, 6 ichneumonids (1 *Ichneumon subfuscus*), 2 braconids, 2 sphecids (1 *Crabro* sp.), 1 serphoid, 19 formicids (1 *Formica fusca*, 16 small red ants and 2 small black ants, 1 chrysidid (*Omalus* sp.).

RANA PRETIOSA

Information on the food habits of this species was obtained by a study of the stomach contents of 12 adults from Jasper National Park—4 were collected at Cabin Lake on June 11, 1952 and 8 at Pyramid Lake on June 10 and 11, 1952. The analyses revealed that the diet consists chiefly of arthropods with molluscs being secondary in importance. The bulk of the arthropod material was composed of insects with the main representatives being Coleoptera and Diptera.

The details of our analyses are presented.

MOLLUSCA—27 snails.

ANNELIDA—1 earthworm.

ARTHROPODA: ARACHNOIDEA—16 spiders, 2 mites (1 oribatid and 1 tyroglyphid), and 1 millipede. INSECTA (159 specimens). Plecoptera—1 nymph; Ephemeroptera—7 nymphs and 1 adult; Odonata—1 damselfly nymph and 3 dragonfly nymphs; Hemiptera—2 lygaeids (*Sphragisticus* sp.); Homoptera—1 fulgorid nymph; Neuroptera—2 larvae and 1 nymph; Coleoptera—5 carabids, 1 dytiscid larva, 3 hydrophilids (1 larval), 2 silphids (*Silpha trituberosa*) and 1 larva, 3 staphylinids, 1 cantharid, 2 elaterids, 1 dermestid (*Byturus unicolor*), 1 byrrhid, 3 chrysomelids, 1 scolytid, 4 undetermined adults; Trichoptera—1 caddis fly larva and 2 adults; Lepidoptera—4 cutworms, 2 moths, 1 each of geometrid and pyralid caterpillars, and 1 undetermined caterpillar; Diptera—47 tipuloids including 3 adult craneflies and 44 winter gnats, 3 larval and 2 adult chironomids, 2 larval culicids (1 each of *Anopheles* and *Aedes* types), 1 larval and 2 adult mycetophilids, 2 larval stratiomyids, 1 calobatid, 9 sepsids, 1 agromyzid, 1 chloropid, 1 larval and 4 adult tetanocerids, 4 larval and 1 adult metopiids, 2 undetermined adult Diptera (acalyptrate); Hymenoptera—1 tenthredinid larva, 3 ichneumonids, 1 brachonid, 1 serphoid, 11 small red ants, and 1 bombid.

BUFO BOREAS

The specimens used in the study of this species included 9 adult and subadults of which 8 were collected at Gorge Creek between July 18 and August 18, 1953, and 1 from Spray Lakes June 4, 1949. Both of these localitiees are in the eastern portion of the Rocky Mountains. The stomach contents were entirely arthropod in nature and consisted mainly of insect material. It seems apparent that Coleoptera and Hymenoptera constitute the main source of food. These orders are represented chiefly by ground beetles and ants.

The results of the analyses are indicated below.

ARTHROPODA: ARACHNOIDEA—10 spiders and 3 centipedes. INSECTA (577 specimens). Orthoptera—2 cave crickets (*Ceutophilus* sp.), 3 truxaline and 4 oediponine grasshoppers; Odonata—1 dragonfly nymph; Hemiptera—2 coreids, 3 lygaeids (1 *Geocoris bullatus* and 1 *Lygriocoris diffusus*), 1 nabid (*Nabis ferus*), 1 mirid, and 4 saldids (*Salda bouchervillei*); Homoptera—1 cicadellid; Coleoptera—18 carabids (7 *Platynus* sp., 2 *Harpalus* sp., 3 *Bembidion* sp., and 1 *Pterostichus* sp.), 1 silphid, 4 staphylinids, 2 elaterids (1 larval), 1 dryopid, 1 coccinellid (*Coccinella transversoguttata*), 1 cerambycid, 5 chrysomelids, 16 curculionids (14 *Otiorhynchus sulcatus*), and 6 undetermined (1 larval); Lepidoptera—8 caterpillars (1 sphingid); Diptera—3 tipuloids (1 cranefly and 2 winter gnats), 1 helomyzid, 3 muscids, and 1 metopiid; Hymenoptera—1 tenthredinid, 1 gasteruptiid, 476 formicids (67 *Camponotus herculeanus*, 89 *Formica fusca*, 194 *F. sanguinea* and 126 undetermined small red or black ants), 3 vespids (*Vespula maculata*), 1 sphecid, 1 anthophorid (*Anthophora* sp.), 1 apid.

AMBYSTOMA TIGRINUM

Our investigation of this species involved 6 specimens collected from the prairie region of southern Alberta—2 from Barons taken in August, 1951, 2 from Brant August 31, 1951 and 2 from Orion August 3, 1953. One stomach contained possible remains of a mollusc but otherwise the contents showed nothing but arthropod material which was almost exclusively insect in nature. One of the specimens from Orion had remains of 1 cricket nymph and 2 large grasshoppers, 2 nabids, 2 cicadellids, 1 coccinellid, 1 moth, and 2 flies in its stomach. The rectum of this same specimen contained portions of 4 grasshoppers, 1 spider beetle and 1 leaf beetle, 2 leaf hoppers and 1 spider. One of the Barons specimens had only a single large ground beetle (*Harpalus* sp. 13.5 mm long) in its stomach.

In view of the small number of specimens involved, we would hesitate to make generalizations regarding the food of tiger salamanders. However, it is apparent that certain individuals were feeding heavily on Orthoptera and also were utilizing substantial quantities of Coleoptera. Furthermore, they seem to prefer the larger items as food material. Like other amphibians, these animals take a wide variety of insect material and it may well be that Orthoptera and Coleoptera constitute the mainstay of the tiger salamander diet.

The details of our analyses follow.

MOLLUSCA—appeared to be remains of 1 specimen.

ARTHROPODA: ARACHNOIDEA—represented by 1 tyroglyphid mite. INSECTA (20 specimens). Orthoptera—4 grasshoppers (2 *Melanoplus bivittatus*, 1 *M. packardi*, and 1 *Melanoplus* sp.), 1 cave cricket (*Ceutophilus*), and 1 cricket nymph (*Gryllus campestris*); Hemiptera—1 gerrid and 2 nabids (*Nabis ferus*); Homoptera—3 cicadellids; Coleoptera—1 carabid (*Harpalus* sp.) and 1 coccinellid; Lepidoptera—1 moth; Diptera—2 borborids, 1 metopiid (*Sarcophaga* sp.), 2 undetermined (1 acalyptrate).

As a result of the present studies we conclude that the over-all picture of the diet of *Rana sylvatica* and *R. pretiosa* is very similar to that of *R. pipiens* and *Pseudacris nigrita*. All of these species appear to subsist mainly on beetles and flies. *Bufo boreas* on the other hand feed chiefly on beetles, especially ground beetles, and hymenopterans represented principally by various kinds of ants. The diet of *B. boreas* is quite comparable to that of *B. hemiophrys* in Alberta and also that of four other species of toads in Oklahoma as reported by Smith and Bragg (Ecology 30:333-349, 1949).—J. E. MOORE AND E. H. STRICKLAND, University of Alberta, Edmonton, Alberta, Canada.

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